ON THE BIOGEOGRAPHIC ECOLOGY OF THE MALAYAN SUN BEAR

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A dissertation submitted to the University of Cambridge in partial fulfilment of the conditions of application for the degree of Doctor of Philosophy

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June 2005

This work is dedicated to the fond and inspirational memory of Schizo, whose young life was cut short tragically by poachers in the forests of East Kalimantan, Borneo, and in whose prophetic life and hug are pure wisdom and meaning.

> Selemat Jalan, Lawai

PREFACE

This research was conducted at the Wildlife Research Group in the Faculty of Biological Sciences under the supervision of Dr David Chivers. This dissertation is the result of my own work (copyright © 2005), and includes nothing which is the outcome of work done in collaboration or by others, except where specifically indicated in the text. No part of this dissertation has been submitted previously to this or any other educational institution for any degree or diploma. The main body of this dissertation does not exceed the page limit set forth by the Faculty of Biological Sciences, University of Cambridge.

Dave M. Augeri Cambridge, UK 24 June 2005

Update: The original dissertation, data, and analyses for this research were stolen on 8 May 2005 and could not be presented in their complete original form for final submittal in June 2005. Although the original cannot be replaced, some portions of this manuscript that could be amended with available data were revised closer to their original form after June 2005.

Dave M. Augeri Denver, CO 25 June 2006

SUMMARY

Both natural and anthropogenic factors can influence bear ecology and habitat use. The character, size, distribution, and availability of suitable habitat will either facilitate or limit a bear's use of critical resources, ultimately affecting its persistence and evolutionary potential. For this study, I compared natural patterns of Malayan sun bear (*Helarctos malayanus*) habitat selection, ecology and landscape use with the effects of disturbance. I conducted two phases of field work during 2000 – 2004 at 16 study sites grouped among 3 focal areas in the Leuser Ecosystem (ca. 24,000 km²) in northern Sumatra and 3 focal areas in the Kayan Mentarang/Bulungan ecosystems (ca. 18,226 km²) in East Kalimantan, Borneo. A representative sample of 50 habitat types and biogeographic conditions, 44 disturbance types, and 60 human activity types were surveyed. Habitat types and biogeographic conditions in undisturbed primary forests similar to those examined in disturbed areas within the same ecosystems were used as control treatments.

Phase I consisted of bear sign censuses *via* Distance- and Fixed-width transect sampling, primary sun bear forage productivity and diversity surveys, tree stand and micro-habitat surveys, and genetic sampling of scat and hair. Phase II entailed a remote camera capture-recapture and presence-absence study for population density and abundance estimates and to test sign survey efficacy. I tested site occupancy probabilities and the frequencies, densities, encounter rates, and detection probabilities of distinct sun bear sign and photographic events as relative indices of habitat use. I conducted a total of 335 km of transects, 512 km² of camera trapping, and 64.2 ha of fruit and tree stand surveys across the 16 study sites as well as an additional ca. 1,200 km of pre- and post-transect surveying. A total of 4,886 sun bear sign events were recorded *via* sign census transects and 10,804 remote photographs were taken over 15,897 trap nights, 107 of which were distinct sun bear photo events.

The direct and interactive effects of habitat disturbance on sun bear ecology and landscape use were consistently the most significant influences across all other variables and tests, regardless of habitat type, ecosystem, biogeographic condition, habitat productivity, site, area, or region. The type, intensity, age, and geographic extent of disturbances accounted for the significant majority of variance in sun bear sign and photo capture events. The most significant effect was the interaction between the age of, and distance to, intensive habitat disturbance (i.e. forest clearing) relative to where and when bears were active. Logging, agriculture, and persistent human activity by trails, hunting, non-timber forest product harvesting, and so forth, were the most statistically-significant factors associated with habitat use by bears, with 92.7% of all bear signs observed in undisturbed forest.

As the level, intensity, and extent of disturbance increased, significantly less bear activity was observed. When examined across all sites, < 10% of signs were observed in secondary forests and only 0.73% were in areas < 15 years old. The significant majority of signs in secondary forests were in forests > 25 years old. A total of 6.8% of signs were observed in the same general area as post-disturbed sites (0-30 years old) and 86% of these were > 500 m and 74% were > 1,000 m from any form of disturbance. Only 2.4% of all signs were observed within 50 m of disturbed areas < 1 year old. No photographs or genetic samples were observed in secondary forests of any age, or in conventionally logged forests, agricultural areas, roads, edge habitats, or other disturbed areas.

Disturbance also created a form of habitat compression that may be inducing density-dependent spatial patterning among bears and subsequently aggregating bear activity in those sites. Human activities had significant effects on bear habitat use and a form of virtual fragmentation (i.e. avoidance of areas without habitat disturbance or hunting) may be occurring. Overall, results showed that sun bears in these study sites were choosing security over food, which has implications for their persistence.

Results indicate the sun bear in these sites is primarily an interior forest-dependent species with a strong affinity for mature, diverse, and heterogeneously structured primary forests. Tests of biogeographic influences in undisturbed forests revealed that mature tree stand characteristics were prominent variables in micro-site and habitat-type selection by sun bears. Tree densities were low to moderate, while tree species diversity, maturity, girth (dbh), height, number of emergents, and canopy cover were all significantly higher in those stands with significantly more bear activity and indicated a strong preference for older and more complex primary forest character. These mature stand traits, especially a predominance of mature fruiting trees, high tree species diversity, and escape cover were the most statistically significant effects on bear habitat use in 97% of undisturbed sites and were important indicators of interior forest affinity for bears.

Consistently-occupied sun bear habitat in these sites is mainly in remote and less accessible primary forests at elevations between 400 - 1,000 m asl, most likely due to intense disturbance and human use in highly productive lowland habitats < 500 m asl. Such ranges appear to be limited to specific areas within undisturbed primary forest and older secondary forest (> 25 - 30 years old) and shift on a seasonal and annual basis. Tests showed that due to loss of suitable habitat and avoidance of highly disturbed areas, young secondary forests, and high-human use areas, sun bear ranges are patchy and fragmented across the overall landscape. Consequently, some bears are likely compelled to forage occasionally in agricultural areas. Compared to the overall population, use of agricultural sites and other habitats outside of undisturbed forests was by relatively few bears and tests indicated the significant majority of these bears were of smaller size/age classes.

Presence-absence modelling (McKenzie *et al.* 2002, 2003) of camera-trapping data for all 16 study sites on Borneo and Sumatra were tested and proved to be robust enough to estimate a range of population sizes in these sites. The largest median population estimate with 50% range overlap was $873 \pm SE$ 197.1 adult bears in Kayan Mentarang National Park (1.4 million ha) in East Kalimantan at a density of 0.042 bears/km⁻². In the adjacent unprotected lowland Bulungan Forest (4,226 ha) densities were lower (0.025 bears/km⁻²) with an estimate of $156 \pm SE$ 48.6 adult bears. In Sumatra's Gunung Leuser National Park (800,000 ha) the population estimate was $280 \pm SE$ 61.2 adult bears at a density of 0.023 bears/km⁻². Lower densities in Sumatra and the Bulungan region are likely due to more extensive habitat loss, fragmentation, and hunting. Although hunting occurs in Kayan Mentarang National Park, habitat disturbance is minimal. All estimates accounted for the proportion of consistently occupied habitat, along with gaps between ranges, and are consistent with published densities for the sun bear's closest phylogenetic relatives.

Results indicate that the IUCN Red List (v. 3.1) for *H. Malayanus* can be updated from Data Deficient (DD) to Vulnerable (VU C2ai) in Indonesia. Considering the low abundances in Indonesia, which likely stewards the largest populations and protected areas in the sun bear's global range, the species may be Endangered (EN, based on criteria B1bi-v, C2ai and D) or Critically Endangered (CR, based on criteria B1a and B1bi-v) in regions where they are more isolated. These data also support the CITES Appendix 1 listing that *H. malayanus* probably is in danger of extinction and is or may be affected by international trade. The bear's affinity for primary forest and the increasing rate of forest loss suggest scientifically-based conservation measures should be implemented without delay. A time and space mosaic can help planners create ecologically-sound reserve networks in these fragmented landscapes.

This was the first study of its kind to generate empirically-based density and abundance estimates of sun bears, and this is the first study of bears using presence-absence modelling, such as that proposed by MacKenzie *et al.* (2002, 2003), to produce these estimates. Thus, these estimates only provide an initial baseline, for which further research should validate and examine trends through multi-year mark-recapture studies in representative habitat types and conditions across the bear's range.

Hunting is affecting sun bear populations in some areas, but in Indonesia the most immediate threats to sun bear persistence are presently forest loss and disturbance. Sun bear survival depends on (a) our ability to predict how biogeographic conditions, changing landscape structures, environmental stochasticity, and anthropogenic disturbances affect bear movement and foraging patterns across time and in increasingly patchy landscapes, (b) improving long-term bear access to critical resources and habitat, and (c) implementing species and habitat-specific protective mechanisms at landscape scales.

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ACKNOWLEDGEMENTS

This research would not have been possible without the tremendous help, support, and patience of numerous people over many years, from supervisors to taxi drivers. It is impossible to thank everyone who has helped me and this work along the way. To all involved directly and on the periphery, I offer my most sincere appreciation and thanks.

My deepest and most heartfelt gratitude are for my parents, Janice and Michael, and for my partner, Michelle Klinger, who have provided me with the most important and essential needs in life and for this work: unconditional support, faith, patience, and perspectives. This work could not have been achieved without them.

My sincere appreciation and thanks are for Dr David Chivers, who served as my supervisor at the University of Cambridge and who provided me with essential academic and scientific support, help, and guidance throughout this work, enabling me to integrate science, conservation, and academics. I am also grateful to my Ph.D. examiners Dr William Sutherland and Dr Nigel Leader-Williams for their generous time, insights and help with this final manuscript.

My deep thanks and appreciation are for Dr Charles Jonkel, who has been my good friend, colleague, and teacher, providing me with professional and personal support, guidance, and sage advice, and who has taught me the way of the bear. I am indebted and grateful to Dr Reed Noss and Dr Paul Paquet, who gave me the initial faith, support, and inspiration to launch my PhD studies in large carnivore Conservation Biology. Dr Richard Reading and Dr Brian Miller have been incredibly supportive as colleagues and friends to me and this research from its inception. I am sincerely appreciative and grateful for all of their help and support. I am also very grateful to Dr Lance Craighead who has provided me with help and support as a colleague and friend. Dr Martin Fisher, good friend and colleague and to whom I am very grateful and appreciative, provided valuable advice, reviews, perspectives, and support throughout this work and was there, at the most critical and trying time, to help when this dissertation and data were stolen three weeks before it was due. My thanks are also to Dr Dave Garshelis, who helped me to begin my initial feasibility work on sun bears and who has provided me with insightful advice and feedback during this work. I am also very grateful to Dr Timothy O'Brien and Dr Margaret Kinnaird for their sage advice, kindness, and generous support.

More than 65 field assistants from Indonesia performed some of the most difficult and arduous work in Conservation Biology for this project. These men persevered with dedication under extremely rugged conditions and risked their lives to help accomplish this research. Suffice it to say, this research would not have been possible without their hard work and dedication. In particular, I am indebted and grateful to Tarmizi, Giman, Zul, Ijar, and Rusman in Sumatra and to Oko Jangin (Kapala Adat and my adopted father), Dan Udau, Lis Mayaidi, and Ahmad in Kalimantan.

I owe special thanks to Dolly Priatna for supervising the camera-trapping work in Sumatra and for his kind help and friendship throughout this project. I also thank Rudy for helping supervise the camera-trapping crews and forest rangers in Leuser, who were so critical for this work in Sumatra. Becky Coles was a fantastic help with data entry in Cambridge and I am especially grateful for her many hours of hard work. Jim ZumBrunnen provided outstanding statistical support *via* the Department of Statistics at Colorado State University and I owe special thanks to him for advising and helping with these complex analyses and providing the statistical objectivity so critical for such work. I am also grateful to Dr Rick Knight of the College of Natural Resources at Colorado State University, who enabled me to be a Visiting Researcher and access the great scientific and academic resources there, and to Dr Gary White, Dr Andy Royle, Dr Ken Burnham, Dr Darryl MacKenzie, and Jim Hines who helped with key advice for portions of the modelling.

I am sincerely grateful and appreciative of Dr Marcela Santamaria Gomez, Dr Melvin Gumal, and everyone from the Wildlife Research Group at the University of Cambridge, all of whom provided great friendship, advice, and a mutual learning environment. I owe special thanks to the Department of Anatomy and Darwin College at the University of Cambridge for providing me with this fine education and academic support. I would like to thank the Society of Conservation Biology, particularly Dr Michael Soulé, Dr Reed Noss, and Dr Thomas Lovejoy, for their exceptional work in this field and for their inspiration for me to pursue my work.

I am indebted to the Mission Aviation Fellowship (MAF) based in Tarakan, East Kalimantan, who provided excellent professional air transport for this project and my special thanks and appreciation are owed to my new friends in MAF, the Holsten and Maynard families, who provided us with friendship, a home base, and generous hospitality. I owe special thanks to Dr Biruté Galdikas, who provided valuable support and help during my first research in Borneo in 1990-91, encouraging me to continue with this work. David Stern at the Department of Conservation Biology of the Denver Zoological Foundation provided helpful data entry for the camera-trapping work and I am grateful to him for this and his resourceful help on many other things. I am very indebted to Raffaella Commitante, who provided timely help re-entering and editing some of the scanned portions of this dissertation after it was stolen. Chris Barr, Dr Jonathan Kingdon and Dr Larua Snook have been good

friends and I am grateful for their generous help, support, and hospitality in Indonesia. I thank Gabriella Fredriksson, who invited me to begin my observations of sun bears at the Sungai Wain Protection Forest, and who provided hospitality and engaging discussions about tropical biology long into the night. I would like to thank the Wanariset in Samboja, the Balikpapan Orangutan Society, and the Sungai Wain Protection Forest for their permission to visit that site.

I am indebted to several generous organisations that supported this work. In the USA, my most heartfelt thanks and appreciation are for the Great Bear Foundation and the Institute of the Rockies, both led by Dr Charles Jonkel, which were instrumental with administrative support and funding to help initiate this project and sustain it (and me) throughout its course. I am sincerely grateful to the Department of Conservation Biology of the Denver Zoological Foundation, led by Dr Richard Reading and Dr Brian Miller, which has been highly supportive and generous throughout this research, providing funding, administrative support, and advice. I am deeply indebted to Mr. Roland Dixon and the Harriman Foundation, which was the main funding organisation for this project and without whom this research may not have been possible. I am grateful to the Division of Research and Exploration of the National Geographic Society, which provided important financial support and institutional backing for this research to begin and sustain it through the first few years. I am also grateful to Dr Joshua Ginsberg, Dr Timothy O'Brien, Dr Margaret Kinnaird, and Dr Robert Lee of the Wildlife Conservation Society Asia Programme, which provided timely support, funding, and guidance during this project and at a critical juncture of this research in 2003. I am grateful to the International Bear Association, which provided important funding to aid the preliminary work and genetic analyses.

In Indonesia, my sincere thanks and appreciation are owed to Dr Mike Griffiths, Dr Yarrow Robertson, and Dr Kathryn Monk, who led the Leuser Management Programme (LMU), and who provided essential in-kind, administrative, and logistical support for the field work in Sumatra. The LMU provided all equipment, field assistants, film, and data entry for the camera-trapping study in the Leuser Ecosystem. The LMU also provisioned half of the camera equipment for the camera-trapping study in the Bulungan Research Forest as well as some of the cameras in the Kayan Mentarang National Park site. As my main Indonesian collaborating organisation, the LMU provided an essential home-base, faith, and patience and was instrumental for helping with permits, letters of support, and general support for the often daunting bureaucracy in the region. I am sincerely indebted to the leaders of LMU and to all LMU staff. In East Kalimantan, the World Wildlife Fund (WWF) – Kayan Mentarang Project provided in-kind support, collaboration, a portion of the camera-

trapping equipment and assistants, and a base of operations for the field work in Kayan Mentarang National Park. My appreciation and thanks go to Pa Ignn Sutedja and Stephan Wulffraat for their patience, support, and faith in this work. For the Bulugan Research Forest (BRF) portion of this research, my appreciation and thanks go to Dr Douglas Sheil, Pa Petrus Gunarso, Pa Ismayaidi Samsoedin, and Joris Siermann of the Center for International Forestry Research (CIFOR). CIFOR provided all of the necessary in-kind support for the field work based from the Seturan field station in the BRF, including partial support for field assistant room and board, GIS data, and administrative support in Bogor. I am grateful to the Indonesian Institute of Sciences (Lembaga Ilmu Pengetahuan Indonesia) for providing the necessary permits and administrative assistance to enable this research to happen in Indonesia and I am grateful to the Indonesian Department of Forestry (Departemen Kehutanan, PHKA (Pelestarian Hutanan Dan Konservasi Alam), and Ministry of the Environment (Menteri Lingkungan Hidup), which provided permits for this research in specific locations. I would like to commemorate and thank the life of Pa Ramon of the East Kalimantan Department of Forestry, who died tragically in a car accident with his wife in 2003. My sincere thanks go to these organisations and to all of the staff who have helped along the way.

To all of my friends who were there for me through thick and thin with patience and care, thank you. For superbly well-timed attitude adjustments and perspectives during this work I am deeply indebted to Bob Hollister, Mike Roselle, Twilly Cannon, Woody Beardsley, Bob van Belle, Dr Charles Jonkel, Chris Barr, Dr Jonathan Kingdon, Dr Laura Snook, Michael Brown, Andrew Brown, John Bowen, team ICE, Ryan Mannix, Kelly Colfer, Dr Suie Ackerly, Ray and Susie Risho, John Wason, Leon Arouth, Sandy Valenzano, Linda Lightfoot, the Augeri family, the Holsten family, the Maynard family, the Peterson family, the Perruccio family, and Joshua Tree.

In addition to being my best friend and partner, Michelle Klinger, also helped with some of the most tedious tasks of data entry and administration of this project, sacrificed life as she knew and loved in Montana to live out of boxes and backpacks in the rain-forest in desperate conditions and discomfort, took care of life's daily needs so that I could focus on this work, and was there for me, this work, and the bears with beautiful and inspirational spirit and perspective. I am deeply appreciative and grateful. Thank you, Michelle ("Soleang"), for all of your patience, support, and sacrifice.

Finally, my deep appreciation are owed to my friends Ganja, Ucil, and Schizo, sages of the rainforest, who showed me the way of the bear.

A note to the thieves who stole this work:

Nil desperandum...

Nil illegitimis carborundum.

CHAPTER 1

INTRODUCTION AND OBJECTIVES



"For thousands of years, the bear has been our companion on our journey on the Earth. More than any other animal, it is the icon and poetry of wildness...It enters our minds, profoundly influencing our dreams and imagination...Its fantastic biological reality carries us into that state of grace and sacredness so necessary for our survival as fully human beings." Shepard (1994)

INTRODUCTION AND OBJECTIVES

1.1 Introduction

The sun bear (*Helarctos malayanus* Raffles, 1821) is the only bear species inhabiting equatorial lowland rain forest (Servheen *et al.* 1999), but due to habitat loss, disturbance, and human-caused mortalities its global population may be less than 25% of historic levels and it is restricted to isolated and fragmented sub-populations (Servheen 1999a). For remaining sun bears, the size, character, distribution, and availability of suitable habitat will either facilitate or limit their use of critical resources, ultimately affecting their fitness, genetic viability, and persistence (Saunders *et al.* 1991, Frankel and Soulé 1992, Servheen *et al.* 1999, Waits *et al.* 1999). Both natural and anthropogenic factors can influence bear ecology and habitat use and it is important to identify accurately the most distinct and interactive influences on these dynamics. Generalisations from limited or biased information can damage both the species and the conservation mechanisms intended to protect it. For bears, forage, habitat character, landscape features, competition, security, habitat loss, and fragmentation are influential in varying degrees (Servheen *et al.* 1999). Thus, the focus in this study was to identify and predict the most dominant influences affecting sun bear biogeographic ecology and, thereby, its persistence and evolutionary potential.

The geometry of an organism interacting with its environment plays a major role in determining its optimal use of landscapes (MacArthur and Pianka 1966). Survival for most animals requires the ability to access suitable habitat, resources, mates, cover, security, and territory across the landscape. Natural biogeographic and environmental conditions can influence these needs, particularly where habitat and forage abundance, diversity and availability are affected. For the majority of bear species, food availability and diversity, habitat condition, and cover are frequently the most prominent ecological factors influencing habitat use. Individuals and populations are also vulnerable to both stochastic and anthropogenic perturbations, which can change continuous forests into a fragmented matrix of disturbed, lost, and unsuitable habitat. Resource loss and habitat disturbance from drought, fire, floods, or fragmentation can affect survival rates of bears and other large carnivores and can lead to genetic, demographic, and population-level impacts (Rogers 1976, Harris 1984, Augeri 1994, Noss et al. 1996, Craighead et al. 1995, Craighead and Vyse 1996, Seidensticker et al. 1999, Merrill et al. 1999, Waits et al. 1999, Laidlaw 2000, Murrow 2001, Crooks 2002, Larkin et al. 2004). Recent studies and reports indicate that sun bears may be seriously affected by such influences (Santiapillai and Santiapillai 1996, Servheen 1999a, Whitten et al. 2000, Augeri, 2003, Meijaard et al. 2005).

For species like sun bears with coevolved adaptations to specific habitat types, natural and anthropogenic factors can influence access to, and the density and abundance of, food and other resources (Augeri 2003, Meijaard et al. 2005). Such loss or limited availability of otherwise suitable habitat for bears can lower habitat carrying-capacities, fragment and isolate populations (Merrill et al. 1999, Murrow 2001, Maher et al. 2003, Larkin et al. 2004), and limit demographic exchange among populations (Craighead and Vyse 1996, Waits et al. 1999). These influences can shift the bears' movement dynamics and affect their habitat use (Mattson et al. 1987, McLellan and Shackleton 1988, Mattson et al. 1996, Merrill et al. 1999, Boyce 2000, Augeri, 1994, 2003, Meijaard et al. 2005). Consequently, health, mating, recruitment, and population dynamics can be affected (Jonkel and Cowan 1970, Rogers 1976, 1987, Craighead et al. 1995, Powell et al. 1997). Loss of, and reduced access to, high-quality resources and habitat, whether from biogeographic or human-causes, can increase physiological stress (Frid and Dill 2002, Wasser et al. 2004), reduce individual survival and reproductive rates (White et al. 1999), create insular effects (Craighead and Vyse 1996, Larkin et al. 2004), and affect bear fitness and persistence (Rodgers 1976, Mattson et al. 1987, Craighead et al. 1995, Powell et al. 1997, White et al. 1999, Boyce et al. 2001, Freedman et al. 2003).

It is clear that accurate scientific information will enable greater success for sun bear conservation plans (Santiapillai and Santiapillai 1996, Augeri 1998, Servheen 1999a, 1999b, Peyton *et al.* 1999). In addition to the paucity of information regarding many aspects of basic sun bear ecology until now, there has been little known about the impacts of biogeographic conditions, landscape structure, and human disturbances on sun bear habitat use, resources, ecological relationships, densities, distributions, isolation, behaviour, and basic life-history (Servheen 1999a). Because the last remaining sun bear populations exist in increasingly human-dominated landscapes, the persistence of sun bears and tropical forests in general are inevitably linked to how ecosystems are managed (Meijaard *et al.* 2005). Indeed, the persistence of local sun bear populations depends on our ability to predict how biogeographic conditions, changing landscape structures, environmental stochasticity, and anthropogenic disturbances affect bear movement, foraging patterns, and access to critical resources in increasingly patchy landscapes over the long-term.

1.2 Addressing the Issues

The 1999 IUCN Bear Specialist Group report notes that, in the Tropics, a lack of basic information regarding bear ecology, habitat loss, fragmentation, and human-caused mortality inhibits managers' abilities to prioritise threats and develop strategies to address the most important issues (Peyton *et al.* 1999). Biological information is a major influence on the development and implementation of conservation plans, but *Helarctos malayanus* is listed as "Data Deficient" on the 2003 IUCN Red List of Threatened Animals (Hilton-Taylor 2003). Accordingly, the 1999 Bear Specialist Group recommended that "basic research on the sun bear is the highest priority need" (Servheen 1999a). Without such information, the establishment and implementation of scientifically-sound conservation plans is difficult and, in fact, the 1999 Bear Specialist Group predicted this species will disappear from many regions before its existence is even documented (Servheen 1999a). The IUCN Malayan Sun Bear Conservation Plan (Servheen 1999a) states:

"The sun bear is the least known of the world's bears. Basic research on the status, ecology, food habits, and distribution of the sun bear is needed everywhere in its range in Southeast Asia...There are no readily available measures of changes in density of sun bears in tropical habitats...(and) there is a need for site-specific application of methods to assess distribution, density, and the impacts of forest harvest on sun bear populations in representative habitats throughout the range of the species...A method to quantify presence/absence and encounter frequency would be useful not only for sun bears but for many other tropical forest mammals such as Felidae. Such a method would allow assessment of distribution and the relative abundance of species in undisturbed and disturbed habitats...(and) is needed to assess the impacts of forest conversion on biodiversity and carnivore survival. This information is needed to develop management and conservation plans that address the needs of resident wildlife..."

The sun bear's globally-threatened status requires timely proactive science and conservation. Given that most sun bears are limited to small isolated populations, environmentally-stochastic events, such as aseasonal fruiting or primary forage crop failures, can negatively affect the survival and persistence of isolated populations. Disturbance and fragmentation are also important influences throughout the bear's range and can act independently and synergistically at both local and landscape scales when coupled with stochastic events. This interaction will affect the sun bear, its ecological relationships, and its influences on tropical forest dynamics as a primary competitor, seed disperser, and predator.

In addition to international and intrinsic mandates for its conservation, the sun bear is an excellent species for tropical forest conservation. The bear's broad niche, spatial requirements, inter-specific relationships, and functional roles qualify it as an "umbrella species" (Noss *et al.* 1996), under which a myriad of tropical animal and plant species, as well as threatened ecosystems, can be conserved. Scientifically-based conservation strategies will enhance the persistence of this ecologically-important species and will facilitate the conservation of many other threatened and endangered species, as well as important ecosystem services for the wider forest community. Ultimately, the persistence of the sun bear, as well as biodiversity and healthy tropical forest dynamics, depend on our understanding of the bear's biogeographic ecology in disturbed and undisturbed landscapes.

The costs of not conserving this species are extensive, but the benefits are immeasurable. Bear conservation helps conserve healthy watersheds, hydrologic and ecosystem processes, and genetic diversity and evolutionary potential for numerous species beyond its own range, including for humans (Herrero 1999, Craighead 2000). For example, Peyton (1999) estimated that focussing conservation strategies on preserving the Andean bear (*Tremarctos ornatus*) and its varied range would conserve 40% of all species present.

Such conservation extends far beyond the environment (Western et al. 1989, Peluso 1992, Peyton 1994, Noss et al. 1996, Augeri 1998b, Herrero 1999, Peyton et al. 1999). History proves that healthy environmental integrity and public awareness help maintain strong political, social, and economic systems. The primary reason South American governments established conservation units for spectacled bears was to preserve watersheds for urban populations (Peyton 1999). In fact, Andean governments continue to define watershed deterioration as an issue of significant national security, causing shortages in food production, drinking water, transportation capacities, hydro-electric power, and employment. The ability to govern and to generate long-term solutions hinge on good conservation and will reduce resource shortages as well as economic, social, and political unrest (Peyton 1999). Such conservation strategies depend on scientifically-sound and pragmatic information, but sun bears and many species, habitats, and indigenous human communities that can be protected by sun bear conservation, may decline unless prompt and accurate scientific studies and conservation plans are implemented (Santiapillai and Santiapillai 1996, Servheen 1999a, Meijaard et al. 2005).

To mitigate bear/human conflicts in South-East Asia's human-dominated landscapes, accurate data on the sun bear's use of, and displacement from, specific habitats in various biogeographic and disturbance conditions are required for conservation plans, where conservation requirements may displace or limit human needs of the same landscapes Chapter 1

(Diamond 1986, Western *et al.* 1989, Woodroffe and Ginsberg 1998, Noss 1991, Servheen *et al.* 1999). Given the rapid decline of forest systems throughout the world and the resulting conservations implications, the principal objective in this study was to examine the biogeographic ecology of sun bears in undisturbed and disturbed habitats. My main questions were focussed on identifying the primary factors that either aid or restrict sun bear habitat and landscape use, i.e. what biogeographic and anthropogenic parameters affect sun bear habitat use, ecology, and distributions across temporal and geographic extents?

Sun bears have evolved under diverse biogeographic conditions and a key to their persistence has been access to suitable habitat. If bears are not able to access resources, this can create fragmented or isolated populations resulting in weakened metapopulation dynamics. The consequences are potentially high risks to population persistence (Frankel and Soulé 1992, Augeri 1994, Waits *et al.* 1999). Thus, a main objective was identifying the most important influences on sun bear habitat use. By understanding what factors influence sun bear habitat use, further insight is possible into how biogeography and disturbances interact to affect the fitness and persistence of sun bears and possibly other species.

1.3 <u>Research Summary</u>

The focus in this study was to compare natural patterns of, and disturbance effects on, sun bear habitat use and ecology between two independent populations that have similar access to both disturbed and undisturbed habitats. Borneo and Sumatra are the best regions in South-East Asia to conduct this comparison within the same ecosystems (Augeri 1999). Parameters associated with forage diversity and availability, cover, competition, predation, topography, and other biogeographic parameters across different habitat types and conditions were compared with logging, agriculture, trails, roads, development, and other human activities. A forage diversity and abundance index, along with fruit productivity and other indices, were developed to examine potential primary forage influences on sun bear habitat use. Camera-trapping and sign data were used in new site occupancy and detection probability models to develop density and distribution estimates of sun bear sub-populations. Diversity models were used to quantify bear demographic diversity, sympatric competitor and predator diversity, and tree species diversity, among others. Undisturbed habitats were used as control sites to test similar areas within the same ecosystems subject to disturbances.

I tested site occpuancy probabilities and the frequencies, densities, encounter rates, and detection probabilities of distinct sun bear sign and photographic events as relative indices of habitat use. Data were used to examine the central themes of four general theories and two formal hypotheses as applied to bears, which form the theoretical and conceptual framework for this study (Chapter 3): (1) Island Biogeography Theory, (2) Foraging Theory,(3) Metapopulation Dynamics Theory, (4) Stress Theory, (5) Perturbation-Stress Hypothesis, and (6) Risk-Disturbance Hypothesis. Specific research questions are noted in section 1.7.

The elusivity of the sun bear and difficulties using conventional wildlife study techniques, such as telemetry in the sun bear's remote, rugged, and densely-canopied habitats, are primary reasons why there is minimal information on this species. These issues were addressed in this study by testing and progressing the integration of site occupancy, detection, and encounter probability modelling with rigorous bear sign censuses, habitat and tree stand surveys, and capture-recapture photographic and genetic analyses. Two phases of field work were conducted at 16 study sites grouped among 3 focal areas in the Leuser Ecosystem (ca. 24,000 km²) of Sumatra and 3 focal areas in the Kayan Mentarang/Bulungan ecosystems (ca. 18,226 km²) on Indonesian Borneo. Phase I consisted of bear sign censuses *via* Distance (line-transect) and Fixed-width transect sampling, forage productivity and diversity surveys, tree stand and micro-habitat surveys, and genetic sampling from scat and hair. Validation tests of sign age and potential habitat biases were conducted throughout the study. Phase II entailed a remote camera capture-recapture study to (a) develop relative population and distribution estimates and (b) test sign census efficacy.

Over a 32-month survey period in 2000 - 2004, a total of 335 km of transects, 576 km² of camera trapping, and 64.2 ha of fruit and tree stand surveys were conducted across the 16 study sites in addition to ca. 1,200 km of pre- and post-transect surveying. A total of 4,886 sun bear sign observations were recorded *via* sign censuses and 10,804 photographs were taken over 15,897 trap nights, 107 of which were distinct sun bear photo events. Analyses examined the complex dynamics of sun bear habitat use in contiguous *versus* patchy landscapes and how various disturbances and biogeographic factors affect their use of these areas across time and space.

1.4 Historic Context

Sun bears historically ranged throughout most of South-East Asia (figure 1.1A), as far east as Borneo and Java and north into Nepal, India, Bhutan, southern China, and eastern Tibet (Servheen 1999a), sharing its range north of Malaysia with the Asiatic black bear (*Ursus thibetanus*) and the sloth bear (*Melursus ursinus*) (Garshelis *et al.* 1999, Servheen *et al.* 1999, Servheen 1999a). Historic habitat for the sun bear encompassed most of South-East Asian terrestrial ecosystems, from sea-level peat swamps and lowland tropical hardwood forests < 500 m above sea level (asl) to lower and upper montane forests above 1,350 m asl (Payne *et al.* 1985, Stirling 1993, Servheen 1999a). During this study, sun bears Chapter 1

in Aceh province, northern Sumatra were documented by camera-trapping at elevations as high as 2,143 m asl in Gunung Leuser National Park and in East Kalimantan, Borneo at 1,450 m asl in Kayan Mentarang National Park. Payne *et al.* (1985) reported sun bear occurrence as high as 2,300 m asl on Gunung Kinabalu in the state of Sabah, Malaysia and Meijaard *et al.* (2005) report an upper range of 2,700 m asl. Although sun bears still inhabit many of their historic habitat types and elevations, this study and other authors (*see* Stirling 1993, Santiapillai and Santiapillai 1996, Servheen 1999a, Whitten *et al.* 2000, Meijaard *et al.* 2005) suggest the bear's primary habitat is tropical lowland hardwood forests below 750 m asl. These forests, however, are highly prized for timber production and are rapidly being logged as well as converted to gardens (primarily fruit and rice), commercial plantation agriculture (e.g. rubber, coffee, tea, corn, oil palm, timber), and settlements (MacKinnon *et al.* 1996, Meijaard 1997, Servheen *et al.* 1999, Whitten *et al.* 2000, Augeri 2003, van Schaik *et al.* 2001, Robertson and van Schaik 2001, WRI 2004, Meijaard *et al.* 2005).

Prior to 1900, anthropogenic impacts on sun bears were primarily related to direct killing, but impacts from habitat loss over the past 100 years have increased substantially and are a major threat to sun bears throughout their range (Santiapillai and Santiapillai 1996, Servheen 1999a, Augeri 2003, Meijaard *et al.* 2005). The latter is a consequence of increasing human populations and the demand for timber, gas, oil, precious metals, jewels, agricultural lands, roads, and living space (Santiapillai and Santiapillai 1996, MacKinnon *et al.* 1996, Herrero 1999, Cincotta and Engleman 2000, Whitten *et al.* 2000, WRI 2004). Based on analyses of habitat loss across the sun bear's range over the previous 100 years, the 1999 IUCN Bear Specialist Group stressed that the sun bear population is significantly below its historic population and range levels (figure 1.1) and is threatened by increasing mortality (Servheen 1999a). By the late 1980's, Servheen (1989) indicated that sun bears were seriously threatened and their situation today is worse (< 25% remaining), primarily due to increases in human-induced mortalities and habitat loss (Servheen 1999a).

The most recent public estimate by the IUCN Bear Specialist Group for the global sun bear population was < 5,000 individuals (Servheen 1999b) but, considering the sun bear is listed as "Data Deficient" on the 2003 IUCN Red List of Threatened Animals (Hilton-Taylor 2003), more data have been needed to validate this estimate. Results of this study provide sufficient data on abundance levels (Chapter 6) and the IUCN Red List status for *Helarctos malayanus* can be updated (Chapter 7). It is clear that sub-populations are limited to small isolated pockets in Myanmar, Thailand, Laos, Vietnam, Kampuchea, and perhaps India/Bangladesh and southern China, while larger, but fragmented populations exist in Malaysia and Indonesia (figure 1.1B) (Santiapillai and Santiapillai 1996, Servheen 1999a).

(A)



(B)



Figure 1.1. (A) Estimated historic distribution of the sun bear. (B) Estimated current sun bear distribution predicted to be islands of habitat patches within the range shown. (From Servheen 1999a).

1.5 Principal Issues

Indonesia and Malaysia preside over some of the largest contiguous blocks of sun bear habitat remaining in the world and, therefore, they probably steward the largest sun bear populations (Santiapillai and Santiapillai 1996, Servheen 1999a). These two countries, however, are also the world's leading producers and exporters of tropical hardwoods (WRI 2001, 2004), most of which originate in the sun bear's primary lowland forest habitat (Santiapillai and Santiapillai 1996, Servheen 1999a). Sun bear population data in Indonesia and Malaysia have been sparse until now and have indicated patchy distributions on Borneo and Sumatra (Santiapillai and Santiapillai 1996, Servheen 1999a). The persistence of these populations depends on large protected areas (Santiapillai and Santiapillai 1996, MacKinnon *et al.* 1996, Leuser Management Unit 1999, Servheen 1999a), two of which (Kayan Mentarang and Gunung Leuser National Parks) provided opportunities in this study to compare remote undisturbed populations as control treatments against disturbed areas within the same ecosystems.

Many factors influence the distribution and abundance of animals, including forage, competition, predation, topography, and the location of suitable habitat. For some individuals and species, these influences predominate. Yet, in some regions bears have adapted to constant variation in these conditions as well as to human influences. Such information regarding sun bears has been minimal. Previous studies indicated sun bears primarily occur in primary forests (Wilson and Wilson 1975, Wilson and Johns 1982, Santiapillai and Santiapillai 1986), while Wong *et al.* (2004) stated that the importance of primary forests in sun bear survival is uncertain. Meijaard (1997) and Mills and Servheen (1994) suggest that conflicts with humans, hunting, and illegal commerce of bears and bear parts are key factors affecting sun bear abundance, but several other studies concluded more pervasive influences are habitat loss and disturbance (MacKinnon *et al.* 1996, Santiapillai and Santiapillai 1996, Momberg *et al.* 1998, Servheen *et al.* 1999, Whitten *et al.* 2000, Augeri 2001, 2003, Meijaard *et al.* 2005).

Herrero (1999) and Waits *et al.* (1999) argue that the three primary factors that drive the loss or decline of bear populations, as well as their genetic and evolutionary viabilities, are habitat loss, habitat fragmentation, and human-induced mortality. Although in some areas direct human-caused mortalities are notable, most bear studies indicate these mortalities are directly correlated with increased human access from deforestation, resource extraction, roads and development (Mattson *et al.* 1987, McLellan and Shackleton 1988, Kasworm and Manley 1990, Mattson and Knight 1991, Noss *et al.* 1996, Mattson 1998, Servheen *et al.* 1999, Bader 2000, Murrow 2001, Larkin *et al.* 2004). Deforestation is the primary cause of habitat loss and fragmentation in South-East Asia with consequent species extinctions and biodiversity declines (Whitmore 1997, Laurance and Bierregaard 1997, Bierregaard *et al.* 2001, Laidlaw 2000, WRI 2004). Results of a 22-year investigation by Laurance *et al.* (2002) clearly demonstrated that the effects of fragmentation on tropical forests are substantial, altering forest dynamics, community-wide trophic structure, connectivity, insularity, ecological and ecosystem processes, species richness, and species abundances. Analyses of satellite imagery of Amazonian forest fragmentation over a 10-year period by Skole and Tucker (1993) showed that the area affected by fragmentation and edge effects is more than 150% larger than the actual disturbed area. Couvet (2002) demonstrated that restricted tree gene flow can have deleterious effects on fragmented populations and Hamilton (1999) confirmed similar effects on tropical tree gene flow, which influences the distribution and abundance of major fruit bearing species and, thus, a large number of frugivores like sun bears.

In general, significant damage can occur in both edge and interior forest communities, particularly within the first few months and years of edge creation up to 300 - 500 m interior (Laurance *et al.* 2000, 2002). This is especially true in patches smaller than 1,000 ha (Lovejoy *et al.* 1986, Laurance *et al.* 2001, 2002). Furthermore, the synergistic interactions between fragmentation and the ecological changes caused by logging, fire, environmentally stochastic events, and hunting impose a more significant threat on particular tropical forest species and communities. In Indonesia, Meijaard *et al.* (2005) discuss numerous cases of the negative effects of selective logging on fauna and flora in the Bulungan ecosystem of East Kalimantan, Borneo and, in some cases, such effects were highly significant. Crooks (2002) demonstrated that fragment area and isolation are the two most dominant predictors of mammalian carnivore abundance and distribution in fragmented habitats.

In Indonesia, tropical forests are primarily converted and lost to (1) commercially- or locally-valuable timber harvests; (2) extraction processes for minerals, precious metals, jewels, and other resources; (3) transmigration projects; (4) family and industrial agriculture; (5) urbanisation; (6) development; (7) living space; and (8) roads (MacKinnon *et al.* 1996, Whitten *et al.* 2000, Robertson and van Schaik 2001, WRI 2004). Any remaining forest fragments often border or are isolated in a surrounding landscape matrix of degraded habitat, commercial plantations, mines, industry, urban centres, villages, trails, and roads, and are influenced by both biotic and abiotic factors. The latter include substantial increases in edge effects, insularisation, community composition and structural changes, and human activities

such as hunting, poaching, resource harvesting and extraction, trails, forest camps, and settlements (Augeri 1995, Laurance and Bierregaard 1997, Whitmore 1997, Wiens 1997).

While each of these factors decreases biodiversity, each also may affect various aspects of sun bear fitness, genetic viability, and evolutionary potential (Servheen *et al.* 1999, Waits *et al.* 1999). These effects include impacts on (1) demography; (2) population dynamics, abundances, densities, and distributions; (3) mating, fecundity and reproductive potential; (4) physiological stress, physical condition, and survival; (5) recruitment and mortality rates; (6) dispersal; (7) habitat selection; (8) home ranges and movement patterns; (9) immigration and emigration rates and processes; (10) resource and habitat availabilities and uses; (11) diet; and (12) inter-specific interactions (Soulé 1980, Gilpin and Soulé 1986, Allendorf *et al.* 1991, Holt 1997, Hedrick and Gilpin 1997, Craighead and Vyse 1996, Noss *et al.* 1996, Craighead *et al.* 1998, Servheen 1999, Waits, *et al.* 1999, White *et al.* 1999, Murrow 2001, Frid and Dill 2002, Larkin *et al.* 2004, Meijaard *et al.* 2005).

Given the sun bear's diverse niche, particularly as a fauni-frugivore (Fredriksson 1998, Augeri 2003, Meijaard *et al.* 2005), it maintains many functional services for the larger community that could be affected. For example, because frugivorous vertebrates and their digestive systems are the primary vectors for tropical seed dispersal and establishment (Terborgh 1990, Redford 1992), sun bear seed dispersal plays important roles in forest regeneration and maintenance. Sun bear foraging actions for termites and other insects (Fredriksson 1998, Augeri 2000, 2003) also aid ecosystem processes, such as nutrient mixing and breakdown, as well as facilitating soil turnover and generation. The diverse ecology of bears also helps maintain trophic relationships, as well as community structure and dynamics (Jonkel and Cowan 1970, Glasser 1979, Jonkel 1984, Kasworm and Manley 1988, Augeri, 1994, Craighead *et al.* 1995, Mace and Waller 1997, Powell *et al.* 1997). Higher-order relationships that could be influenced by disturbance include altered or lost ecological interactions like predation and competition, which can lead to lateral, hierarchical, and cascading changes across trophic levels (Augeri 1994, 1995, 2003, Soulé and Terborgh 1999, Terborgh *et al.* 1999, Harrison and Bruna 1999).

Although biogeographic conditions and disturbance can be substantial influences on bear food availability and diversity, environmentally-stochastic events like primary food resource failures can also influence bear health, movements, mating, recruitment, and population dynamics (Jonkel and Cowan 1970, Rogers 1976, 1987, Craighead *et al.* 1995, Powell *et al.* 1997), some of which have been observed on Borneo (Wong 2002). Fruit availability is clearly an important factor for sun bears and drought/rain are notable influences on fruit productivity in the tropics, including during El Niño Southern Oscillation

Chapter 1

(ENSO) events (Bebber *et al.* 2004, Condit *et al.* 2004), which can affect dioecious (pioneer) species like figs that are an important resource for sun bears throughout the forest and year (Fredriksson 2001, Augeri 2002, Wong 2002). The effects of such stochastic events, however, can be exacerbated by logging, forest loss, fire, and other disturbances (Laurance 2001, Peres 2001, Laurance and Williamson 2001, Cochrane 2001, Meijaard *et al.* 2005).

Biogeographic conditions can affect the distribution of primary sun bear foods, but timber harvesting produces degraded areas or secondary forests that ultimately change the availability and abundance of key sun bear resources, while plantation development reduces heterogeneous forests to monocultures incapable of supporting sun bears and many other threatened and sensitive species (Servheen 1999a, Laidlaw 2000, Augeri 2003). As a result, carrying-capacities for sun bears and other tropical species may be altered (Servheen 1999a, Laidlaw 2000). Thus, the 1999 IUCN Bear Specialist Group recommended that information is needed on how species like sun bears and other large carnivores adapt to or are impacted by such habitat and landscape changes. For sun bears, forest clearing can:

- (1) Prevent access to more seasonally productive areas or those relatively unaffected by drought or other stochastic events.
- (2) Reduce the diversity, abundance, and availability of key food sources, such as fruit, bee hives, and termites in logged areas, border habitats, and in the core zones of disturbed or disturbance-affected home ranges.
- (3) Exacerbate the effects of drought both locally and regionally by inducing micro-climatic changes.
- (4) Create the effects of drought or influence other local micro-climate conditions, such as changes in temperature, humidity, wind, and light incidence, which impact plant biology and, thus, seed, flower, and fruit productivity in interior and edge forests.
- (5) Provide access for hunters.

These and other effects can influence the nutritional stability of sun bears and where they can move and forage across the landscape, particularly for those bears that are restricted to small forest reserves or patches.

1.6 Prior Conservation Action and Recommendations

Helarctos malayanus has been listed as Data Deficient on the IUCN Red List since 1996 (Hilton-Taylor 2003) and it has been listed on Appendix I of the Convention on International Trade in Endangered Species of Wild Flora and Fauna (CITES) since 1979. Indonesia, Malaysia, and Brunei became Parties to CITIES in 1979, 1978, and 1990 respectively and the sun bear has been protected by Indonesian law since 1973, but several researchers in the region suggest these laws and their implementation do not properly address sun bear habitat conservation, poaching, or trade (MacKinnon *et al.* 1996; Santiapillai and Santiapillai 1996, Momberg *et al.* 1998, Meijaard 1999, Whitten *et al.* 2000, Meijaard *et al.* 2005). There have been no conservation strategies, mechanisms, or plans actually implemented specifically for sun bears, nor any habitat conservation expressly focused on sun bears. Essentially, conservation plans in the region do not adequately address these issues, lack enforcement, and are devoid of much scientific data.

According to the IUCN Bear Specialist Group, the goals for most of the world's bear populations, including for sun bears, are to maintain habitat and linkages between populations, minimise direct and indirect human-caused mortalities, and increase public support for bear conservation (Servheen *et al.* 1999). It is also recommended by many conservation biologists and organisations in the region that both scientific and conservation information should be available for local people who both directly and indirectly affect conservation (Meijaard 1997, Saeed *et al.* 1998, Augeri 1998a, 2000, 2001, 2003, Servheen *et al.* 1999, Herrero 1999, Peyton *et al.* 1999, Leuser Management Unit 1999, WWF pers. comm.). Such information should be provided in the forms of public presentations and fora, posters, brochures, videos, and other multi-media sources (Augeri 1999, I. Sutedja pers. comm., Leuser Management Unit 1999)

Servheen (1999a) strongly recommended the need for methods to quantify presence/absence and encounter frequency, as well as site-specific methods to assess distribution, density, and the impacts of forest harvest on all aspects of sun bear populations across their range. This is particularly important for assessing sun bear relative abundance and distribution in undisturbed *versus* disturbed habitats. In addition, Peyton *et al.* (1999) advise that information is needed on how and to what degree human activities impact the capacity of habitat to provide critical needs for bears, such as the distribution and seasonality of bear foods, availability of security cover, size and shape of habitat blocks, and presence of corridors to connect sub-populations and resource needs. The 1999 Bear Specialist Group report also recommends that obtaining multiple genetic samples throughout the sun bear's range is a high priority (Waits *et al.* 1999). Results and methods from all of this work are

valuable for sun bears and other Ursidae, as well as for many other carnivores and forest dependent mammals.

1.7 Study Goals and Objectives

1.7a Specific Goals

- The primary research goals in this study were to (A) test natural patterns of, and disturbance effects on, sun bear use of resources, suitable habitat, and the overall landscape matrix and (B) generate data by non-invasive methods on sun bear biogeographic ecology, inter-specific relationships, and relative densities and distributions.
- 2) Improve methods for studying elusive or rare species by direct and indirect wildlife study methods combined in rigorous sampling designs and analysed with theoretical and empirically-supported models and robust statistical schemes.
- **3)** Develop scientifically-sound and pragmatic recommendations for regional conservation plans that incorporate cultural, socio-economic, and political factors across the bear's range.
- **4)** Develop and provide conservation education, capacity-building, and training programmes to enhance public awareness and local career development.

1.7b Specific Objectives and Questions

Objective 1: Sun bear Ecology, Habitat, and Landscape Use

In Phase I the basic ecology of the sun bear was studied for 32 months between 2000 – 2004 across varying temporal and geographic scales. The primary data collection methods were: (a) sign censuses by Distance (line-transect) and Fixed-width transect sampling, (b) forage productivity and diversity surveys, (c) habitat and tree stand surveys, and (d) capture-recapture and presence-absence analyses from camera-trapping and scat and hair genetic samples. Data were used to analyse the bear's use of different resources and habitat types and its role in the ecosystem. Quantification included, for example, analyses of bear signs/ unit area between disturbed and undisturbed habitat types. Specific research questions were:

- 1) Do biogeographic conditions differ among sites most used and avoided by bears?
- 2) Do tree stand character and diversity differ among habitats most used and avoided by bears?
- **3)** Does dominant (i.e. most frequently occurring) sun bear habitat structural character differ among the most frequently used and avoided sites?
- 4) Does primary sun bear forage differ among the most frequently used and avoided habitats and sites?
- 5) Do conditions such as topography, elevation, and cover differ among the most frequently used and avoided habitats and sites?
- 6) Does the presence of primary sun bear competitors differ among similar disturbed and undisturbed habitat types?
- 7) Does inter-specific competitor presence affect sun bear habitat use?
- 8) Does sympatric antagonistic species presence differ among similar disturbed and undisturbed habitat types?
- 9) Does sympatric antagonistic species presence affect sun bear habitat use?
- **10)** Do sun bear sign detection probabilities differ in different biogeographic conditions and between disturbed and undisturbed sites?
- **11)** Does disturbance affect primary sun bear forage and resource use in similar biogeographic conditions?
- **12)** Does disturbance affect fruit productivity, diversity, distribution or abundance in similar biogeographic conditions and habitat types?
- **13)** Does disturbance affect primary sun bear forage diversity, distribution or abundance in similar biogeographic conditions and habitat types?

Objective 2: Sun Bear Density, Abundance, and Distribution

In Phase II bear sign densities and population estimates were generated for the focal areas from the densities and distributions of sign census and capture-recapture photo data across different habitat and disturbance types in each study area. Analyses were conducted in Distance (Buckland *et al.* 1993, 2001) and presence-absence models (MacKenzie *et al.* 2002, Royle and Nichols 2003) using encounter frequency, detection probability, and site occupancy probability modelling. A primary assumption was that a higher abundance of bears results in higher incidences of distinct bear signs and photographs in similar habitat types and environmental conditions. Specific research questions were:

- 1) Do encounter frequencies vary between different habitats and disturbed and undisturbed sites?
- 2) Are sun bear ranging patterns affected by disturbance in similar biogeographic conditions and habitat types?
- **3)** Do sun bear sign densities differ among disturbed and undisturbed habitat types in similar biogeographic conditions?
- **4)** Do sun bear population densities differ among disturbed and undisturbed habitat types in similar biogeographic conditions?
- 5) Are sun bears evenly distributed within sites and across the landscape?

Objective 3: Analysis of Biogeographic and Disturbance Effects

Although it has been reported that sun bears prefer primary forests, studies on other bear species and reports from Indonesia and Malaysia also suggest that, under specific conditions, bears sometimes use gardens, plantations, logged, or marginal areas. Data gathered from sun bear sign censuses, camera-trapping, and genetic samples were analysed to test the hypothesis that biogeographic conditions, disturbances, human activities, and habitat fragmentation influence sun bear ecology and habitat use patterns across the landscape. Several general questions were:

- a) Do biogeographic conditions influence bear habitat use and site occupancy?
- b) Does fragmentation or disturbance reduce suitable habitat availability?
- c) Do biogeographic conditions or disturbance create insular effects on sun bear population dynamics, such as sub-population compression and metapopulation structure?

d) Do disturbance, fragmentation, and biogeographic conditions affect various aspects of sun bear populations, such as densities and distributions, food habits, resource use, habitat quality and use, and ranging patterns?

Analyses were focussed on biogeographic and landscape features that provide suitable habitat and aid or disrupt bear use of resources and movement between preferred areas. New presence-absence and site occupancy models specifically adapted for this study were used to examine where and to what degree bears were consistently occupying specific habitat types and whether habitat fragmentation and isolation affect sun bear populations. Specific questions were:

- 1) Do site-occupancy rates vary between different habitat types and disturbed and undisturbed sites?
- 2) Does edge affect sun bear habitat use and movements through the landscape?
- 3) Does disturbance affect sun bear habitat use in similar biogeographic conditions?
- 4) Do human presence and activities affect sun bear habitat use and landscape movements?
- 5) Does disturbance affect sun bear movement patterns in the landscape?
- 6) Do roads and trails affect sun bear movements through the landscape?
- 7) Do sun bear sign densities and distributions vary in different disturbed and biogeographic conditions?
- 8) Do sun bear population densities and distributions vary in different disturbed and biogeographic conditions?
- **9)** Does disturbance affect overall sun bear landscape use in similar biogeographic conditions and habitat types?
- **10)** Is the sun bear population continuous or fragmented into geographically isolated sub-populations?

Objective 4: Local professional development

A main project objective was to enhance the capacity of Indonesian citizens through knowledge and skill-sharing, technical, scientific, and conservation training programmes, and conservation ecology education. Given the extensive and diverse knowledge of indigenous people in these areas, it was also a major objective for mutual and cross-cultural knowledge and skill-sharing. This occurred in several forms, including:

- 1) Collaborative partnerships with Indonesian colleagues, organizations, and government departments on portions of this and other projects.
- 2) Development of professional Indonesian biologists through skill-sharing and collaboration on portions of this and other projects.
- **3)** Training, employment, and capacity-building of Indonesian field staff by data collection and field work.
- **4)** Working with and employing only local Indonesian biologists and indigeneous forest-dwelling people with life experience and knowledge in forest and wildlife ecology in these particular study areas.

Objective 5: Public Education

Public education programmes, such as school and university lectures, community presentations, and training programmes were important objectives, as they offer fora for input and ownership, education in sun bear and tropical ecology and conservation, and the tools to build capacity for, and implementation of, conservation goals at local and national levels. These programmes were provided to all local communities where I worked, as well as to all Indonesian-based collaborating organisations.

Objective 6: Scientific Recommendations and Conservation Planning

Results from this research are being applied to sun bear and tropical forest recommendations for further research and conservation planning. Guidelines and planning strategies are being provided to local governing bodies and collaborating organizations to include a diversity of species', ecosystem, and socio-political needs. Recommendations include disturbance mitigation measures, conservation strategies, land uses planning, and methods for wildlife studying and monitoring.
CHAPTER 2

SUN BEAR

EVOLUTION



AND

BIOLOGY

SUN BEAR EVOLUTION AND BIOLOGY

2.1 Sun Bear Evolution and Taxonomy

As members of the order Carnivora, the Ursidae family evolved from smaller, treeclimbing predatory ancestors (Miacidae) about 25 million years ago (mya) (Herrero 1999). All eight species of modern bears today share a common ancestor, *Ursavus*, which evolved in sub-tropical Europe during the Miocene period over 20 mya (Craighead 2000). During the Miocene epoch, ursavine bears increased in size and their dentition shifted from a faunivorous diet to one more like today's bears with broad flat molars (Ward and Kynaston 1995), indicating a more frugivorous and herbivorous diet.

Three lines of modern bears emerged from *Ursavus* (figure 2.1). The majority of molecular studies include the giant panda (*Ailuropoda melanoleuca*) within the Ursidae family and the most current phylogenetic reconstructions among the eight Ursidae place it as the oldest modern bear species (Gittleman 1999, Waits *et al.* 1999). Giant pandas split from the main *Ursavus* line and evolved from *Agriarctos* approximately 20 mya (Ward and Kynaston 1995). Molecular analyses conclude that the next modern bear to evolve was the spectacled (Andean) bear (*Tremarctos ornatus*) (Waits *et al.* 1999), which split from *Ursavus elemensis* around 14 mya (Ward and Kynaston 1995) and is the only South American bear today (Nowak, 1991, Stirling 1993, Craighead 2000).

The direct progenitor of the third bear line, which is the subfamily Ursinae or true ursine bears, was *Protursus*, having evolved from *U. elemensis* between 12 - 10 mya. The first true ursine bear, *Ursus minimus*, evolved from *Protursus* and appeared about 5 mya (Ward and Kynaston 1995). MtDNA sequence analyses suggest the sloth bear (*Melursus ursinus*) as the first modern ursine lineage to emerge, but the branching order of the remaining species is uncertain (Waits *et al.* 1999, Gittleman 1999).

Sun bears likely evolved in South-East Asia from the main lineage of ursine bears (*U. minimus*) about one million years after the sloth bear line branched (Craighead 2000), but the phylogenetic placement of sun bears among the Ursidae remains unclear. MtDNA analyses by Zhang and Ryder (1994) indicated sun bear and American black bear (*Ursus americanus*) species diverged as sister taxa after the sloth bear and the next to evolve was the Asiatic black bear (*Ursus thibetanus*). However, Waits (1996) found the branching order among the sun bear, American black bear, and Asiatic black bear could not be statistically resolved with a 95% confidence interval. The latter could be the result of a rapid radiation event among these three species (Waits *et al.* 1999).



Figure 2.1. Evolutionary history and phylogenetic hierarchy of bears and their closest relatives (modified from: Ward and Kynaston 1995, Waits *et al.* 1999).

Opinions vary about keeping the sun bear in its own genus, *Helarctos*, or to include it in the genus *Ursus* (Meijaard 2004, Meijaard *et al.* 2005), which is already composed of four species. It is currently listed officially by the IUCN Species Survival Commission, the IUCN/IBA Bear Specialist Group, the IUCN Red List, and by CITES as *Helarctos malayanus*. Based on cranial variation among a handful of sun bear specimens from different parts of South-East Asia, Meijaard (2004) suggests that the Bornean race may be a distinct sub-species and proposes it should be called *Ursus malayanus euryspilus*, but the quantity and gender of specimens from Borneo examined in that study were limited. Furthermore, cranial variation is not the only taxonomic consideration for sub-specific distinctions, particularly for Ursidae, which have a large degree of morphological and physiological variation and have inter-bred, producing reproductively viable offspring. Nevertheless, if this distinction is supported, then Meijaard proposes that other sun bear populations should be within *Ursus malayanus malayanus* (Meijaard 2004, Meijaard *et al.* 2005).

At the height of its distribution (figure 1.1A) it is assumed that the mainland sun bear populations were connected by contiguous habitat (Craighead 2000). The sun bear also inhabited most of the islands west of Wallace's Line, which marks the edge of the continental shelf between Borneo and Sulawesi and a division between Asiatic and Australian fauna and flora (Wallace 1880, Craighead 2000).

Throughout geologic evolution, ocean levels have never been low enough to enable a land bridge between Borneo and Sulawesi, effectively limiting most terrestrial animals' abilities to migrate further east or west (Wallace 1880). It is assumed, therefore, that ancestral sun bear populations became isolated on Sumatra and Borneo from the Malay Peninsula in periods of higher sea levels during the Pliocene epoch about 5 mya (Craighead 2000). There are no fossil records of sun bears east of Wallace's Line and it is believed that if some sun bears did cross this deep ocean trench, they were never able to establish successful populations (Craighead 2000). Although the sun bear persists in isolated forest pockets from Myanmar to Borneo (figure 1.1B), it does not exist on any islands other than Sumatra and Borneo. Today, the sun bear is the only bear inhabiting Malaysia, Indonesia, and Brunei and equatorial lowland rain forests anywhere on Earth (Servheen *et al.* 1999).

2.2 <u>Sun Bear Morphology</u>

Sun bear morphology is unique among the Ursidae (figures 2.2 and 2.3). It is the smallest bear in the Ursidae family with an average adult body length of 1.1 - 1.5 m, weight of 30 - 65 kg, and shoulder height of 70 cm (Pocock 1941, Stirling 1993, Meijaard 1997). Typical among Ursidae, sun bears are sexually dimorphic, with males generally 10 - 20% larger than females (Pocock 1941, Payne *et al.* 1985, Meijaard 1997).



Figure 2.2. Malayan sun bear in East Kalimantan, Indonesia. Photo taken by remote camera trapping in Kayan Mentarang National Park. \bigcirc 2003 Dave Augeri and WWF – Kayan Mentarang Project.



Figure 2.3 Malayan sun bear at a road-side wildlife attraction in East Kalimantan, Indonesia.

The sun bear's head and neck are large, wide, and heavy in proportion to its body and its palate is broad in proportion to its skull, yet its ears are small and round (figures 2.2 and 2.3) (Servheen 1999a, Stirling 1993, Pocock 1941). Its muzzle is shorter and lighter coloured than its most similar-looking cousin *U. americanus* and, in general, the white area around the muzzle extends above the eyes (Stirling 1993). It has an exceptionally long tongue that can be extended 20 - 25 cm during feeding (Meijaard 1997), which is useful for extracting termites, ants, and honey. The bear's teeth, particularly the canines, are considered quite large for its body size (Servheen 1999a), but it is primarily frugivorous and secondarily insectivorous (Payne *et al.* 1985, Stirling 1993, Augeri 2002, 2003). The soles of its feet are naked and its front feet are turned significantly inward with long heavy claws, all of which are adaptations for climbing, tearing into trees and logs, and digging for termites, ants and other insects (Stirling 1993, Servheen 1999a).

Sun bear hair length is the shortest of any bear species and is dominated by a black pelage that can vary from reddish to gray (Payne *et al.* 1985). Virtually all sun bears have a chest patch in the shape of a "U", circle, or spot that ranges from yellowish and orange to white (Pocock 1941, Stirling 1993, Meijaard 1997). Craighead (2000) suggested this patch may be a secondary sexual characteristic for attracting the opposite sex or it may be an important part of a threat display. It is also assumed by some biologists that the morphology of these patches is unique for each bear (D. Garshelis pers. comm.).

2.3 Sun Bear Biology

2.3a Prior Research

Meijaard *et al.* (2005) summarise the full body of research presently available on wild sun bears. Including the current study, sun bear research in the wild consists of four concurrent full-time field studies, all beginning in 1997 – 1999, and one part-time study currently in progress. One project (Fredriksson 2001, 2005) was focused on the effects of fire on sun bear foraging ecology in East Kalimantan. Wong (2002) studied basic sun bear ecology and home range patterns in Sabah and a third study examined oil palm plantation use by sun bears in Sabah (Normua *et al.* 2003, 2004). A part-time study on sun bear and Asiatic black bear ecology and sympatric habitat use is on-going in Thailand (Steinmetz, in progress).

Fredriksson's (2001, 2005) study was in the small 10,000 ha Sungai Wain Protection Forest in East Kalimantan and encompassed qualitative work on sun bear rehabilitation and quantitative study using telemetry on 3 habituated and 3 wild bears, faecal analyses, and habitat traits related to sun bear diet. The latter was relative to the effects of forest fires on termites and fruiting phenology (G. Fredriksson pers. comm.). Wong's work was located within a 43,800 ha protected area surrounded by logging concessions in the Danum Valley of Sabah, Malaysia, and entailed a 1 ¹/₂ year trapping and remote photograph M.S. thesis study to generate general information on sun bear ecology (Wong 2002, Wong *et al.* 2004). Normua studied the seasonal movements of four radio-collared sun bears in and around an oil palm plantation in Sabah, Malaysia (Normua *et al.* 2003, 2004).

Despite significant and high-quality efforts, sun bear capture success rates by Wong (2002), G. Fredriksson (pers. comm.), and Normua *et al.* (2003, 2004) were minimal and sample sizes were low. Although a total of 14 wild sun bears have been captured for research purposes across four different projects [3 bears in East Kalimantan (G. Fredriksson pers. comm.); 6 bears in Sabah (Wong 2002); 4 bears in Sabah (Normua *et al.* 2004); 1 bear in Thailand (D. Garshelis pers comm.)], this required extensive multi-year trapping efforts resulting in only a 42.8% success rate (n = 6 bears) of full-time telemetry data for more than six months. The remaining eight bears in these studies were lost or died.

2.3b <u>Reproduction</u>

There are no quantitative data regarding sun bear reproduction in the wild. Based on captive bears, oestrus is estimated to begin at 3 years of age, but first parturition may be at about 5 years (Meijaard *et al.* 2005.). Stirling (1993) reported that cubs are born throughout the year in captivity, which has been verified in Indonesia (pers. obs., G. Fredriksson pers. comm.), and Dathe (1970) noted one zoo report of two successful births to a single female in one year – all indicating possible aseasonal breeding (Meijaard *et al.* 2005). According to Dathe (1970), females are capable of pregnancy soon after they loose a cub. Gestation periods for captive sun bears are recorded to range from 90 to 240 days, of which the upper time length suggests delayed implantation consistent with other bear species (Stirling 1993).

Local people in Indonesia report that sun bears give birth and/or rear young cubs in hollow logs or other secure natural cavities at the base of large trees (pers. obs., Meijaard *et al.* 2005). The significant majority of such evidence in the present study was in primary forest and was rare in secondary forest younger than 30 years. After reports of locals observing an adult sun bear fleeing from inside a hollow log in Sungai Wain Protection Forest, East Kalimantan, evidence was found of a possible young or new-born cub in the log (G. Fredriksson, D. Garshelis, pers. obs. 1998). There was no evidence of the mother or cub's return and it was assumed that the mother likely abandoned the log due to human disturbance. It is unknown whether the cub reunited with the mother or if it was abandoned,

lost, died, was predated, or was taken by local people. Like other Ursidae, sun bear mothers most likely wait until the cub is weaned and large enough or has died before having another (Nowak 1999).

Captive litters have consisted of one or two cubs weighing an average of 325 grams each (Nowak 1991) and either one or two cubs have been observed with adult females in the wild (G. Fredriksson pers. comm., Nowak 1999, Meijaard *et al.* 2005). Camera-trapping in the present study captured one instance of a female with two yearling cubs in Kayan Mentarang National Park, whereas other photo captures of females accompanied by apparent offspring were of one cub.

2.3c Foraging Ecology

The feeding ecology of sun bears is "omnivorous", with a principal diet as a faunifrugivore largely consisting of fruit, termites, ants, bee honey, larvae, beetles, earthworms, and occasionally small animals, mushrooms, succulent plants, and flowers (Lekagul and McNeely 1977, Payne *et al.* 1985, McConkey and Galleti 1999, Wong 2002, Augeri 2002, 2003, Fredriksson 2001). It appears that fruit comprises the primary food resource for sun bears. At least 113 species of fruit were recorded in the sun bear diet in the Sungai Wain Protection Forest, East Kalimantan and *Ficus* spp. were the most frequently occurring fruits in the bear's diet during inter-mast periods (G. Fredriksson unpubl. data as cited in Meijaard *et al.* 2005). Results from the current study showed over 772 tree species were used by sun bears in East Kalimantan, Aceh, and North Sumatra and the most frequently selected trees were from the families Dipterocarpaceae, Euphorbiaceae, Fagaceae, Lauraceae, Moraceae, Myrtaceae, and Sapindaceae with an average dbh of 50.83 cm (*see* Chapter 5). It appears that fruits from the Fagaceae family (oak) may dominate the bear's frugivorous diet at higher elevations (Davies and Payne 1982, Augeri 2003, Meijaard *et al.* 2005).

At least 48 species of termites and 60 ant species were documented in the sun bear's diet in Sungai Wain (Fredriksson and Wich in prep., as cited in Meijaard *et al.* 2005), while Wong (2002) observed a variety of vertebrates in 56 sun bear scats consisting of birds, eggs, reptiles, fish, and several unidentified small vertebrates. Less than 1% of 1,297 scats collected between 1997 – 2003 in southern East Kalimantan by G. Fredriksson (n=1,257) (as cited in Meijaard *et al.* 2005) and in northern East Kalimantan and northern Sumatra (this study) (n=40) contained hair or bone remains. It is unknown how much time sun bears devote to foraging, but several researchers have reported foraging activity as long as 20 hours/day in *U. arctos* and *U. americanus*, particularly in the last months prior to denning

(Jonkel and Cowan 1970, Rogers 1976, 1987, Craighead et al. 1995, Powell et al. 1997, Augeri unpub. data).

On a community level, sun bears are a significant seed disperser, an important ecological component of which is for large-seeded trees (*Durio* spp. *Artocarpus integer*; *Dacryodes rugosa*) (McConkey and Galleti 1999, Augeri 2001, 2003, Fredriksson 2001, Wong 2002). Sun bears are also an important lateral and hierarchical influence on community-wide dynamics through competition, insect and small vertebrate predation, soil turn-over and aeration, nutrient mixing, and biomass decomposition.

2.3d Competitive Relationships

Prior to this study there has been no published information regarding intra-specific competition and density-dependent processes among sun bears (*see* Chapters 5 and 6). The most important competitive influences are probably relative to the bear's frugivorous and insectivorous diet.

More than 50 sympatric fruigivorous and insectivorous vertebrate competitors were recorded overlapping within 10 m of sun bear activity in this study and the most dominant taxa comprised forest ungulates, primates, and birds. Given the highly-diverse fauna of South-East Asia, this is likely a minimum estimate and is limited by human observation. S.A. Wich (pers. comm.) observed a sun bear and orang-utan foraging in the same fig tree near the Ketambe research station in Gunung Leuser National Park. G. Fredriksson (pers. comm.) observed that some ground birds trail sun bears during termite foraging. As an insect competitor, sun bears affect the availability and distribution of live termite nests and ant colonies through significant predation, but they are conservative in their consumption (Augeri 2002, 2003, Fredriksson 2001). For example, G. Fredriksson (unpub. data as cited in Meijaard *et al.* 2005) observed a 50:50 ratio of untouched *versus* foraged termite colonies in the Sungai Wain Protection Forest, East Kalimantan. About 300 live nests/ha of one termite species remained active while an average of 300 nests/ha were excavated by bears. It is certain that bears will influence and be affected by the distribution and/or foraging activities of rival insectivorous species like pangolin (*Manis javanica*).

2.3e Agonistic Relationships

Sun bears evolved with large carnivorous Felidae like tigers (*Panthera tigris sumatrae*), clouded leopards (*Neofelis nebulosa*), and Asian leopards (*Panthera pardus*). The latter species is probably extinct in Indonesia, but it still exists in mainland Asia. The Asiatic golden cat (*Felis temminkii*) is smaller than the other felids, but it is capable of

preying on bear juveniles and cubs and antagonistic interactions probably occur when encountering adult bears. These predators may have influenced the bear's evolution, behaviour, ecology, and time-energy budget relative to predation-risk, including the bear's arboreal foraging and nesting habits. G. Fredriksson (pers. comm.) stated that a reticulated python killed and ate an adult female sun bear under telemetry observation in the Sungai Wain Protection Forest in East Kalimantan, but there is no information on the frequency of such interactions. Other than humans, there are no other local predators on sun bears.

At the minimum, tigers and leopards are presumed to be antagonistic when encountering sun bears (Augeri 2001) and may influence bear habitat use temporally and perhaps spatially. Kawanishi (2002) recorded one sun bear carcass presumed killed by tigers and two tiger scats containing the remains of sun bear(s). The frequency of such antagonistic or predatory interactions is unknown. Geographic overlap to within one metre was observed in this study between sun bears and tigers, clouded leopards and Asiatic golden cats (as well as with marbled cats (*Pardofelis marmorata*), leopard cats (*Felis bengalensis*, and bay cats (*Felis bada*)), but temporal overlap between bears and tigers was at least 3 days apart. The minimum period between photo captures of bears and clouded leopards at the same sites was 6:14 h and for Asiatic golden cats was 30:40 h (Chapter 5).

2.3f Ranging Patterns

In the Danum Valley, Sabah, Wong (2002) recorded mimimum convex pologyon (MCP) home ranges of 4 male sun bears of $6.2 - 20.6 \text{ km}^2$ with an average of 14.8 km². Straight-line daily distances between telemetry coordinates were 141 - 5,660 m (Wong 2002). Fredriksson and Wich (in prep. as cited in Meijaard *et al.* 2005) report a daily range of 8 km in Sungai Wain, East Kalimantan and a mean home range of $4 - 5 \text{ km}^2$. Normua *et al.* (2004) reported minimum MCP home ranges for two male and two female sun bears were $1.2 - 5.1 \text{ km}^2$ near an oil palm estate in Sabah, but these telemetry survey efforts were limited to only about 1 - 2 km around the estate. The latter home ranges were mainly in interior forest and were expected to be much larger (Normua *et al.* 2004).

Sun bears probably do not migrate, but may alter their ranges across seasons and years according to food availability, such as during local and seasonal fruiting events and mast-fruiting or when shifting to alternative food sources during low fruiting years (Augeri 2003). It is assumed that, like other Ursidae, many female sun bear ranges will overlap with their mothers while other females and most males disperse to new ranges, although ranges of both genders can overlap with other bears. Wong (2002) estimated overlap among four telemetry surveyed male bears varied from 0.54 km² to 3.45 km². G. Fredriksson (pers. comm.) and

Meijaard *et al.* (2005) report females with cubs, siblings, and occasional "groupings" at large food sources (e.g. large fruiting *Ficus* spp.). Although the frequency and extent of sun bear aggregation is unknown, it is likely minimal and parallels other Ursidae, where the majority of adult bears without cubs follow relatively solitary behaviour patterns.

The majority of sun bear activity is concentrated in lowland and hill dipterocarp forest below 750 m asl (Davies and Payne 1982, Fredriksson 2001, Augeri 2002, 2003, Wong 2002, Normua *et al.* 2003, 2004, Meijaard *et al.* 2005), but sign and camera-trapping data from this study show bears and bear activity in lower and upper montane forests as high as 2,143 m asl in North Sumatra and 1,450 m asl in East Kalimantan, Borneo. Payne *et al.* (1985) reported sun bear occurrence as high as 2,300 m asl, while Meijaard *et al.* (2005) note an upper range of 2,700 m asl. Sun bear activity has rarely been observed in recently logged or burned areas (Augeri 2003, Fredriksson and Wich, in prep. as cited in Meijaard *et al.* 2005) and the bear's activity patterns encompass diurnal and nocturnal behaviour. Although Normua *et al.* (2003, 2004) tracked movements of 4 bears by telemetry in and around an oil palm plantation in Sabah, 100% of bear activity around the estate was nocturnal and the majority of bear activity (88%) was in primary forest at least 1 km from the edge (Normua *et al.* 2003). Griffiths and van Schaik (1993) found that sun bears shifted their activities to nocturnal behaviour in areas with higher human activity in northern Sumatra.

2.3g Biogeographic Ecology

Habitat Structure: Forage, security cover, and suitable habitat are frequently cited as the most important natural variables influencing bear ecology and habitat use (*see* Jonkel and Cowan 1970, Rodgers 1976, 1977, McLellan and Shackleton 1988, Nowak, 1991, Mattson *et al.* 1991, 1996, Stirling 1993, Augeri 1994, Craighead *et al.* 1995, 2001, Powell *et al.* 1997, Merrill *et al.* 1999, Bader 2000, Craighead 2000, Meijaard *et al.* 2005). Several studies report that sun bears are mainly a primary forest-dwelling species (Fetherstonhauh 1940, Wilson and Wilson 1975, Wilson and Johns 1982, Johns 1983, Augeri 2001, Meijaard *et al.* 2005), where the most dominant traits are mature and diverse forest structure with a high basal area of emergent and fruiting trees, full canopy cover, high escape cover, and diverse and abundant forage (Augeri 2003, Meijaard *et al.* 2005). Wong et al. (2004) state that the importance of primary forest for sun bear survival is uncertain.

Topography is generally insignificant for bears, physically, but in many regions slope, aspect and elevation significantly influence bear forage type and productivity. In general, the highest abundances of bears throughout the world are correlated with

undisturbed habitats of varying types that are in mature to late successional stages with heterogeneous biogeographic structure, moderate to high cover, and access to large ranges with considerable and diverse forage productivity (Servheen *et al.* 1999). Biogeographic conditions, environmentally-stochastic events, and anthropogenic disturbance affect these resources for sun bears in Indonesia, particularly cover and the availability, abundance, and diversity of primary bear forage (Augeri 2003, Meijaard *et al.* 2005, Fredriksson 2005). Although sun bears are principally associated with primary forests, escalating habitat and forage losses are increasingly dominant influences on sun bear ecology and habitat use (Augeri 2003, Wong *et al.* 2004, Meijaard *et al.* 2005, Fredriksson 2005).

Cover: For most bear species, access to, and the spatial configuration of, cover are vital for their persistence (Mattson and Knight 1991, Stirling 1993, Augeri 1994, Craighead *et al.* 1995, 2001, Powell *et al.* 1997, Mattson *et al.* 1987, 1996, Merrill *et al.* 1999, Boitani *et al.* 1999, Servheen *et al.* 1999, Bader 2000, Meijaard *et al.* 2005). Female bears generally have a higher affinity for cover and secure habitat, but most studies show that all bears are susceptible to human-induced mortality, especially in or near open or exposed habitats, roads, trails, and sites with moderate to high levels of human use (*see* Servheen *et al.* 1999). Recent studies in East Kalimantan and northern Sumatra suggest sun bears are particularly prone to such mortalities in areas with increasing forage and habitat losses (Augeri 2002, 2003, Meijaard *et al.* 2005).

For bears, fragmentation generally lowers the effectiveness of preferred habitat (Bader 2000). Blanchard and Knight (1991) found that female grizzly bears (*Ursus arctos horribilis*) with yearlings chose security over more productive habitats in the Yellowstone Ecosystem. Human-caused or related mortality accounts for more than 85% of grizzly bear mortalities in that ecosystem (Bader 2000) and secondary roads were five times higher in mortality risk for all bears than in interior areas without roads (Mattson and Knight 1991). For sun bears, mature primary forests with extensive and high cover are dominant influences (Meijaard *et al.* 2005) and perceived risk appears to be an important variable in their habitat selection. Loss of suitable habitat, however, leads to increased conflicts between people and sun bears in some parts their range (Augeri 2001, 2002, Fredriksson 2005).

Forage: Both spatial and temporal availabilities of food are critical for sustaining healthy physiological and reproductive condition in bears. Mast fruiting, mass insect hatching, fish migrations, and prey-calving are important for northern bears to build fat reserves to survive long hibernation (Jonkel and Cowan 1970, Rodgers 1976, 1977, McLellan and Shackleton.

1988, Stirling 1993, Craighead *et al.* 1995, Powell *et al.* 1997). Mast-fruiting is critical for tropical bears to survive long inter-mast periods (Meijaard *et al.* 2005, Fredriksson 2005) or maternal denning.

Because all bear species can be highly susceptible to prolonged periods of primary forage loss, they need unrestricted access to resources on a constant basis throughout the landscape to enhance their fitness (Rogers 1976, 1987, Kasworm and Manly 1988, Craighead *et al.* 1995, Powell *et al.* 1997, Craighead WWI 2000). Sun bears are no exception. Wong (2002) observed a 33 – 66% mortality of marked sun bears in Danum Valley, Sabah, where the primary cause was suspected to be poor physiological condition from low food availability (Wong 2002, Wong *et al.* 2004). Fredriksson (2005) reported similar forage deficiencies in the Sungai Wain Protection Forest, East Kalimantan. Due to the highly-patchy nature of tropical food resources across variable geographic and temporal scales, especially of primary sun bear forage (fruit, termites, ants, bee hives), data from the current study indicate sun bears may depend on contiguous habitat and landscape features that facilitate unrestricted access to food resources.

Sun bears generally occur where there are diverse, productive, and rich food sources. Poor habitat condition or loss are important and sometimes dominant influences on the ecological dynamics of bears. Small habitat patches are most susceptible to stochastic and human disturbances, which can affect fruiting patterns, productivity, and distribution, as well as access to those resources (Lovejoy et al. 1986, Laurance et al. 2001, 2002). In East Kalimantan, 60% loss of suitable habitat by fires and human encroachment induced sun bears to forage outside of the Sungai Wain Protection Forest, particularly in agricultural areas along forest edges (Fredriksson 2005). Alternating drought and rain are notable influences on fruit productivity in the tropics, particularly on dioecious (pioneer) and other figs, which are an important resource for sun bears throughout the forest and year (Fredriksson 2001, Augeri 2002, Wong 2002). Such pressures render species like sun bears with a predominantly frugivorous diet highly dependent on alternative resources, especially those outside of those areas. In contrast, large tracts of contiguous undisturbed forests support less disturbed and more stable micro-climatic conditions (Lovejoy et al. 1986, Bierregaard et al. 2001, Laurance et al. 2001, 2002). This stability in undisturbed forests increases the availability of fruit-bearing trees across a more accessible and diverse landscape, including during stochastic episodes like fires and El Niño Southern Oscillation events that can affect mast-fruiting in the tropics (Ross et al. 2002, Condit et al. 2004, Bebber et al. 2004, Fredriksson 2005). These episodes would not create as significant an effect in large continuous forests as in smaller forests subject to disturbance and edge effects

(Lovejoy et al. 1986, Bierregaard et al. 2001, Laurance et al. 2001, 2002, Augeri 1995, 2003, Meijaard et al. 2005).

Access to forage, cover, and suitable habitat are clearly important for all bears and these factors appear to be significant influences on sun bear habitat use (Augeri 2003, Meijaard *et al.* 2005). For the majority of bear species, environmentally-stochastic events like resource and habitat losses can influence bear health, movements, mating, recruitment, and population dynamics (Jonkel and Cowan 1970, Rogers 1976, 1987, Craighead *et al.* 1995, Powell *et al.* 1997, Wong 2002). The effects of such stochastic events on bears, however, can be exacerbated by logging, habitat loss, and other disturbances (Mattson *et al.* 1996, Merrill *et al.* 1999, Augeri 2001, 2003, Fredriksson 2005, Meijaard *et al.* 2005). The net result of forest loss and degradation in Indonesia is increasingly fragmented habitats (MacKinnon *et al.* 1996, Santiapillai and Santiapillai 1996, Whitten *et al.* 2000, Laidlaw 2000, Augeri 2003, WRI 2004, Meijaard *et al.* 2005) with corresponding effects of insularity, isolation, and stress on remaining sun bear populations.

CHAPTER 3

THEORETICAL FRAMEWORK





Number of Species

THEORETICAL FRAMEWORK

To address the central questions of this study, four general theories and two formal hypotheses structure the theoretical foundation of this research. Data from this research were not used to formally test these theories; rather, the theories form the conceptual framework of this study and are adapted anew to examine the central questions and potential effects they propose regarding habitat fragmentation, insularity, risk, foraging, and stress relative to sun bears. Accordingly, data were used statistically to test and model various aspects of the central concepts formalised by these theories. Although some aspects of each theory have been debated, their relevance remains particularly germane and applicable to increasingly fragmented and modified landscapes today (Doak and Mills 1994, Wilson 1999, Young and Clarke 2001, Hanski 2001). The fundamental ideas of these theories have inspired a significant paradigm shift along with substantial intellectual and practical applications that have advanced conservation biology, including development of new theories and formal hypotheses. A new framework, defined in this study as the Perturbation-Stress Hypothesis, was inspired by these essential works and is proposed here as a new way to integrate these fundamental concepts. This hypthesis was also developed to view and address the numerous and sometimes synergistic effects that influence the ecological dynamics of particular species and communities.

3.1 Island Biogeography Theory and Population Persistence

Insularity is a pervasive feature of biogeography (MacArthur and Wilson 1967). The effects of insularisation on the diversity, distribution and abundance of species are observed throughout all natural systems – from streams, ponds, and caves to tropical forests, tundra, prairie, and alpine mountain tops. The original theory of island biogeography proposed by MacArthur and Wilson (1963, 1967) attempts to explain these effects in natural island systems across taxa. As a neutral theory, it applies general ecological "rules" affecting all organisms on a *per capita* basis. Its primary goal is to predict ecological patterns and to identify relationships or parameters that potentially account for 85% or more of the variation in species diversity, abundances and distributions (MacArthur and Wilson 1967). Because the central foundation of this theory addresses habitat fragmentation and insularisation, its relevance remains important for the increasingly fragmented and modified landscapes today (Wilson 1999), especially in the tropics (Laurance and Bierregaard 1997, Laidlaw 2000, Bierregaard *et al.* 2001) and for bears and other large carnivores (Harris 1984, Augeri 1994, 1995, Noss *et al.* 1996, Waits *et al.* 1999, Payton *et al.* 1999, Merrill *et al.* 1999, Murrow

2001, Boyce *et al.* 2001), including sun bears (Santiapilli and Santiapilli 1996, Servheen 1999a, Whitten *et al.* 2000, Augeri 2001, 2003, Meijaard *et al.* 2005).

Some tropical species appear to have naturally irregular distributions due to habitat, competition, predation, or climate, but many more species have abnormally patchy distributions caused by habitat fragmentation (MacArthur 1972). It is well recognised that habitat loss and its associated fragmentation form the greatest threat to biological diversity (Laurance and Bierregaard 1997, Bierregaard et al. 2001a), to which numerous rainforest species respond negatively (see Lovejoy et al. 1986, Laidlaw 2000, Bierregaard et al. 2001a, Meijaard et al. 2005). Insularity is a significant and frequent cause of these responses (MacArthur and Wilson 1967, MacArthur 1972, Diamond 1975, Soulé and Wilcox 1980, Harris 1984, Lovejoy et al. 1986, Hanski and Gilpin 1997, Wiens 1997, Bierregard et al. 2001a). Habitat loss and conversions that do not account for the cumulative effects of individual sites across wider temporal and spatial scales can affect the ecology, population dynamics, fitness, and evolutionary potential of individual species (Soulé 1980, Frankel and Soulé 1992) including bears (Mattson et al. 1987, McLellan and Shacklton 1988, Mattson et al. 1996, Noss et al. 1996, Craighead and Vyse 1996, Craighead et al. 2001, Merrill et al. 1999, Waits et al. 1999, Boyce et al. 2001, Meijaard et al. 2005). Although island biogeography theory tends to simplify ecological systems, this is an inherent trait of general theories. Regardless, its applicability remains highly pertinent to habitat fragmentation and the main principles of island biogeography can help explain a substantial portion of the variance in the biogeographic ecology of sun bears in Indonesia.

The basic MacArthur and Wilson (1963) model of island biogeography proposes a dynamic equilibrium between immigration of new species onto islands and the extinction of species previously there, where the size of the islands will drive that equilibrium. Theoretically, species continue to immigrate over an indefinite period, during which time not all are successful in establishing on the island while some residents succumb to extinction. The model helps predict that, while the equilibrium number of species will remain 'fixed', the actual species establishing there will change. Assumptions for the model are that ecological interactions on the island occur as a result of random filling of niches, without adaptations to the presence of interacting species developing there. Thus, evolution is excluded. Importantly, while the basic model is focussed on species-area relationships, a decisive parameter is distance from sources or colonies, such that island faunas become increasingly impoverished as distance increases from the nearest land mass (MacArthur and Wilson 1967, Harris 1984). The basic model is defined as:

 $S = cA^z$

In essence, as the size of the area sampled, 'A', increases across an ecologicallyuniform area, the number of animal or plant species, 'S', increases in an approximate logarithmic manner, where c < 1 and varies among taxa according to the unit of area measurement (MacArthur and Wilson 1963, 1967). The z value (slope coefficient) is a constant that generally falls within 0.2 and 0.35. According to MacArthur and Wilson (1967), the empirically-derived z values are consistent with the independently-derived generalisation that the frequency curve of species with varying populations shows a lognormal distribution. When plots increase in size on the same island or continent, the z values will generally decrease to between 0.12 and 0.17. An important characteristic of this model is that the exchange of individuals is substantially reduced among islands (or patches on a continent) due to barriers (MacArthur and Wilson 1967).

Harris (1984) showed that, if an island or patch were reduced by 90%, the number of species it could support would be halved. If the z value was lowered to 0.14, the area would need to be increased by 140 times in order to support a two-fold increase in species (figure 3.1). Conversely, the z values can be "forced" higher when islands or patches increase in size (MacArthur and Wilson 1967, Harris 1984). According to the theory, extinctions will decline as area increases. If the z value is 0.5, the area needed to support twice as many species would need to be increased by a factor of four (Harris 1984).

In general, as an island or patch increases in area, its topography broadens in complexity, particularly where elevation gradients exist. This progressively increases habitat heterogeneity, which can then support more species assemblies. Consequently, because abundances and the total number of individuals increases with increasing area, species abundances will also rise in a canonical manner (figure 3.2), which will account for any observed increment in insular z values (MacArthur and Wilson 1967).



Figure 3.1. Relationship between the Z exponent value in the species-area equation $S = cA^z$ and the increase in area necessary to double the number of species. (Adapted from Harris 1984).

Distance, however, will exert an important regulatory effect. The dynamic equilibrium in this species-area relationship will be moderated by the distance from an island (or patch) to the closest source of colonisers, where an increase in distance will lower the immigration curve (figure 3.2). This relationship is exhibited well in the Sunda and Polynesian island groups. In their original work, MacArthur and Wilson (1963) compared this distance effect on the species-area relationship for the island groups of Melanesia, Micronesia and Polynesia, where, as distance from the closest faunal source increased, the number of land and freshwater bird species declined, despite a corresponding increase in island size. In contrast, because the Sunda Islands are grouped much closer together, distance has little effect on the species-area relationship.



Figure 3.2. Distance effect on the species-area relationship. As distance increases, immigration rate will decline, whereas an increase in area will lower the extinction rate (Adapted MacArthur and Wilson 1963).

Area will affect extinction rates where larger islands generally have (1) greater habitat heterogeneity, (2) reduced niche overlap and, thus, decreased intensity of interactions, and (3) larger population sizes making chance extinctions less probable. In peninsular Malaysia, Laidlaw (2000) showed that decreasing mammal species richness is positively correlated with decreasing fragment size. Diamond (1969) tested this model in the Channel Islands and found that species turnover might be inversely proportional to population sizes of the species present. Thus, a density-dependent effect may influence extinction rates through competition and niche packing (MacArthur 1972), but Brown and Kodric-Brown (1977) tested this assumption and found that turnover rates were consistently higher on more isolated and distant islands. Thus, repeated immigration into a small population will reduce the probability of extinction, known as the "rescue effect", and when this occurs turnover rates will be directly proportional to distance (Brown and Kodric-Brown 1977).

The rescue effect was originally proposed for mainland-island systems, but it can also be applied to fragmented single-species mainland metapopulations (Soulé and Wilcox 1980, Hanski and Gilpin 1997), including bears (Craighead and Vyse 1996, Waits *et al.* 1999, Murrow 2001). In the tropics of the Malaysian peninsula, Laidlaw (2000) showed that larger carnivores and herbivores that occurred in continuous primary forest were observed less frequently as the size of forest fragments decreased. Because some species like bears have relatively long generation times, the degree of isolation will determine whether species will persist over longer periods (Laidlaw 2000).

From predictions of when a rescue effect may occur, immigration rates decline exponentially with distance, where the extinction curve bends down as distance between areas decreases. Turnover is thus highest at distances when both immigration and extinction rates are high. Regardless of distance, once the area decreases below a minimum size that can support persistent densities of a particular population, the population will become unstable and a threshold may be reached (MacArthur and Wilson 1967).

Boyce *et al.* (2001) examined an extinction threshold for grizzly bear females with cubs of the year using data for 1959 – 1987 from the Yellowstone Ecosystem population in the contiguous US. Following Dennis *et al.* (1991) and Shaffer (1983), the probability of extinction, π , was estimated based on an arbitrary extinction threshold set for n_e at 10 and 1 for different thresholds. The value for n_e was the number of adult female grizzly bears accompanied by cubs of the year at a presumed time that extinction would occur. The model used was:

$$x_d = x_0 - x_e = \ln(n_0 / n_e)$$

where x_0 is the natural log of n_o and x_e is the natural log of n_e . Using a population trajectory over a time period of t_0 to t_q , the probability of extinction was estimated by:

$$\pi(x_d, \mu, \sigma^2) = 1, \mu \le 0; \exp(-2 \mu x_d/\sigma^2), \mu > 0$$

Boyce *et al.* (2001) then plotted the mean time for the population to reach various extinction thresholds (figure 3.3). The model demonstrated that removing < 25 adult female bears would result in an extinction probability of less than 0.2. But, when 50 or more females were lost from the population, the probability of extinction raised significantly from approximately 0.5 to 1.0. Boyce *et al.* (2001) note that the time to extinction has a skewed distribution and the modal extinction time was a better fit.



Extinction Threshold of Adult Female Grizzly Bears with Cubs of Year

Figure 3.3. The probability of reaching an extinction threshold for the Yellowstone grizzly bear population based on the number of adult females with cubs of the year. In this case, removing < 25 bears from the population would result in a probability of extinction < 0.2. With a loss of > 50 bears, the extinction probability significantly increases from ≈ 0.5 to 1 (Adapted from Boyce *et al.* 2001).

When disturbance is added to a system, negative effects on the equilibria of populations and species will occur. Villa *et al.* (1992) modelled the effect of regular disturbance at differing intensities on species equilibrium. They discovered that autecological traits of individual species are an important component in this relationship. In general, slow-growing organisms never reached equilibrium on large islands, but on small islands these species types reached an equilibrium, but only when there was no disturbance. Essentially, slowly-developing organisms (e.g. bears and other large mammals) could not reach an equilibrium on any islands at higher levels of disturbance. In contrast, organisms that reach maturity at a faster rate could reach equilibrium on any size island, but only in the absence of disturbance. Larger population sizes were possible for pioneer species on very large islands and equilibriums were reached with moderate disturbance levels, but only with more area.

When Villa *et al.* (1992) modelled this relationship at the community level similar effects were observed. In general, disturbance lowered the overall number of resident species, but with sufficient time under zero or minimum levels of disturbance, diversities could equilibrate or increase. At high levels of disturbance, slowly-maturing species were not able to persist, but generalist pioneers or rapid colonisers (e.g. weeds, r-selected growth species, etc.) could establish, which reflected diversities of a relatively homogenous group of species. Relative to the basic island biogeography model, the steepness of the species-area curve increased when disturbance was present, but diversity declined.

Although some of the details of the basic island biogeography model have been criticised, the patterns predicted by the model have been observed across a wide variety of taxa and the underlying dynamics have been verified by experimentation (Simberloff and Wilson 1969, Brown 1971, Lovejoy *et al.* 1986, Johnson *et al.* 2000). Comparing genetic sequence differences between island and mainland alleles, Johnson *et al.* (2000) developed a genetic framework to examine the basic assumptions of the model and made predictions regarding the magnitude of genetic divergence of isolated populations relative to island size and distance from the mainland. Because island biogeography models demonstrate how area affects extinction rates while distance to source populations affect colonisation and immigration rates, the Johnson *et al.* (2000) model expressed the mean genetic divergence relative to island size and distance to the mainland (figure 3.4).

For islands close to source genes, the genetic divergences in the Johnson *et al.* (2000) model were greatly influenced by the probability of new immigrant allele fixing. In other words, populations on larger islands were predicted to contain more alleles with small divergence originating at the time of colonisation, whereas populations on small islands close to source fauna were derived more from recent immigrants (Johnson *et al.* 2000).



Figure 3.4. Relationships between mean genetic divergence across populations as a function of island area (distance held constant) and distance from the mainland (area held constant) (Adapted from Johnson *et al.* 2000).

The majority of alleles in populations on small islands close to source genes were lost, because of a higher fixation probability from new immigrants. The distribution of genetic divergences on large distant islands showed that most alleles descended from the time of colonisation with little fixation from recent immigrants. In contrast, small distant islands showed genetic distributions dominated by new immigrants that have higher probabilities of fixation (Johnson *et al.* 2000).

Ultimately, the underlying patterns and predictions associated with island biogeography remain highly relevant for isolated populations, whether on true islands or in insular mainland patches (Harris 1984). The rise and fall of species or communities depends on the fitness of individual organisms and their ability to persist, reproduce, and recruit new reproductively successful members into their population. Their population persistence and evolution as a species in that area will depend on the carrying-capacity or ability of that isolated island or patch to support its individual members through multiple generations.

Bears and other large carnivores are susceptible to negative genetic, demographic, and population level impacts of isolation (Harris 1984, Augeri 1994, Noss *et al.* 1996, Craighead *et al.* 1995, Craighead and Vyse 1996, Seidensticker *et al.* 1999, Merril *et al.* 1999, Waits *et al.* 1999, Murrow 2001). Recent studies and reports are showing that sun bears are among the most seriously affected (Santiapilli and Santiapilli 1996, Servheen 1999a, Whitten *et al.* 2000, Augeri 2001, 2003, Meijaard *et al.* 2005). The balance between local bear population extinctions and recolonisations within patches define the persistence of the population (Waits *et al.* 1999). In their recent GIS modelling of Florida black bear (*U. americanus floridanus*) fragmentation and insularity, Larkin *et al.* (2004) noted that fragmentation and insularisation will not only affect genetic drift and inbreeding depression, but also bear food resource availability, which can compromise bear fitness (Rodgers 1976). Because fragmentation can depress food resources, bears are also forced outside of protected areas for food, which often results in increased human-induced mortality (*see* following sections).

Isolation can limit demographic exchange among bear populations, lower patch carrying-capacity, and limit the availability of otherwise suitable habitat (Murrow 2001). Because female bears show limited dispersal (Bunnell and Tait 1981, Rogers 1977, 1987, Craighead *et al* 1995, Boyce *et al*. 2001, Lee and Vaughan 2003) and are known more generally to occupy ranges overlapping or adjacent to their mothers (Craighead *et al*. 1995), bears are especially vulnerable to fragmentation and isolation (Servheen *et al*. 1999).

Connectivity among patches is a major influence on the long-term persistence of *Ursus americanus* and *Ursus arctos horribilis*. Murrow (2001) and Anderson (1997) found that habitat patches for American black bears (*U. americanus*) need to be close or well connected

for effective colonisation. Larkin *et al.* (2004) found that forest cover was the most "overwhelming component" for Florida black bear least-cost dispersal pathways, where at least 95% of the pathways with the least amount of cost to the bears crossed core black bear habitat. Beausoleil (1999) discovered that female *U. americanus* movements between patches did not occur if distances were greater than 0.5 km apart. Metapopulation modelling by Murrow (2001) of the southern Appalachian *U. americanus* population showed an isolation distance threshold of less than 15 km, where linear barriers such as highways could increase the isolation effect. Murrow concluded that movement barriers like highways and urban areas may result in under-estimation of *U. americanus* extinction probabilities for patches, even for those with relatively short isolation distances.

Simberloff (1999) notes that suitable corridors will benefit *U. americanus* because of its affinity for forests and hesitation for crossing open spaces. Only one of 500 radiocollared grizzly bears in the contiguous US over a 20-year period moved between subpopulations within a matrix of highly degraded and human-dominated areas, yet it is known that dispersal by bears, particularly young males, can occur at great distances in contiguous undisturbed habitats (Boyce *et al.* 2001). Stratman *et al.* (2001) documented a dispersal distance of 507 km by an American black bear in Florida in a two-month period, indicating how occasional long-distance movements can help the persistence of isolated subpopulations, but barriers such as urban centres, highways, large agricultural areas, and so forth can limit or block such movements (Harris 1984, Augeri 1994, 2003, Noss *et al.* 1996, Craighead *et al.* 1995, Merril *et al.* 1999, Bader 2000, Murrow 2001, Larkin *et al.* 2004, Meijaard *et al.* 2005).

As with other species, dispersing bears help rescue depressed populations by increasing genetic and demographic diversities and by augmenting abundance (Boyce *et al.* 2001, Stratman *et al.* 2001, Larkin *et al.* 2004). When even modest dispersal was included in simulation models (figure 3.5), Boyce *et al.* (2001) demonstrated that the grizzly bear population increased to about 80% of carrying-capacity and the majority of sub-populations approached 100% occupancy after 100 years. An important conclusion is that connectivity will greatly facilitate bear dispersal leading to an improved distribution among sub-populations and a higher probability of long-term persistence (Mattson *et al.* 1987, Mattson and Knight 1991, Craighead and Vyse 1996, Mattson *et al.* 1996, Merril *et al.* 1999, Bader 2000, Boyce *et al.* 2001, Larkin *et al.* 2004).



Migration Rate vs Distance

Figure 3.5. A decay function of migration rate relative to distance used to simulate dispersal of grizzly bears among sub-populations (Adapted from Boyce *et al.* 2001).

Boitani *et al.* (1999) concluded that fragmentation of the European brown bear (*U. arctos*) population in the Eastern Alps and Italy has resulted in: (1) significant reduction in the carrying-capacity for the bear, (2) loss and fragmentation of suitable habitat, (3) interference with seasonal habitat and spatial requirements, and (4) increased potential conflict between bears and humans. A system of connected protected areas was found to be the only alternative solution for bear conservation in the Eastern Alps and Italy. In Italy, a network of linear barriers by roads, highways, and railways has prevented bear movement along as much as 91% of its length. Augeri (1994) found the Trans-Canadian Highway in Banff National Park posed a substantial barrier to large carnivore movements, including of both black bear and grizzly bear, potentially fragmenting their populations and impacting the large carnivore guild, their prey base and wider community dynamics. Boitani *et al.* (1999) stressed that land features and movement barriers on local scales can significantly influence bear movements and, hence, functional connectivity and overall population persistence.

Although environmentally-stochastic events, such as low productivity, can affect some bear populations, this is generally a short-term effect (Jonkel and Cowan 1970, Rogers 1976, 1987, Craighead *et al.* 1995, Powell *et al.* 1997, Boyce *et al.* 2001), with which most bear species have co-evolved. In contrast, isolation and insularity from habitat fragmentation can be more detrimental to the long-term persistence of individual bear populations (Craighead and Vyse 1996, Waits *et al* 1999, Servheen *et al.* 1999, Murrow 2001). Patch size is a significant determinant for individual American black bear persistence at local scales (Murrow 2001, Larken *et al.* 2004). Distance and potential movement barriers between suitable habitat patches are the main determinants for the long-term persistence of local patch sub-populations and the overall American black bear metapopulation in the southern US (Murrow 2001), as well as for the contiguous US grizzly bear population (Boyce *et al.* 2001) and European brown bear population (Boitani *et al.* 1999). For the American black bear, Murrow (2001) concluded that isolation is the primary impediment for persistence. Despite the presence of large occupied areas, bears would not be able to persist unless suitable and accessible habitat connections were present (Murrow 2001). Several studies resulted in similar conclusions for *U. arctos* in North America and Europe (Mattson *et al.* 1987, Mattson and Knight 1991, Craighead and Vyse 1996, Mattson *et al.* 1996, Merril *et al.* 1999, Boitani *et al.* 1999, Servheen *et al.* 1999, Bader 2000, Craighead *et al.* 2001). Considering these studies, as well as those of Augeri (2003) and Meijaard *et al.* (2005), which found sun bear habitat use, foraging patterns, and abundance are influenced strongly by human activity and disturbance, particularly in small or isolated forest patches and reserves, it is likely that island biogeography theory can provide important insights and identify patterns and relationships to predict sun bear densities, distribution, and persistence.

3.2 Foraging Theory and Habitat Selection

The geometry of organisms interacting with their environment plays a major role in determining their optimal use of a patchy landscape (MacArthur and Pianka 1966). An individual will allocate time and energy in the most advantageous fashion to access a three-dimensional patchwork of resources within and across habitats. Traditional theory (McNab 1963, MacArthur and Pianka 1966, MacArthur 1968, Schoener 1971, Smith 1980) suggests that optimal use of energy or time is based on whether the resulting gain in time spent per unit of food exceeds any loss. Time-energy profitability models assume that: (1) feeding rate within patches or niches of uniform resource density rises at a decelerating rate as density increases; (2) when feeding/foraging declines due to low densities of resources, the individual spends more time in areas where profits are greatest; (3) resource use may be depressed in areas of high resource density if competition produces interference; and (4) individuals are capable of feeding on alternate resources (Smith 1980).

Although optimal-foraging theories vary in their assumptions and ability to generalise across taxa, their applicability in forecasting animal behaviour for particular species fits predictions from moderate to excellent (Krebs and Davies 1984). In particular, an important component of foraging theory demonstrates how the loss of feeding patches can predict the carrying-capacities of individual sites and optimal-foraging models can estimate the distribution of organisms in patches of differing profitability. In essence, because foraging behaviour affects population persistence, optimal-foraging theory is useful for understanding and predicting the consequences of resource depletion and habitat fragmentation (Caro 1998), including as it relates to bears.

Foraging theory shows that in habitat patches where food is less abundant, unevenly dispersed, or difficult to access, subsequent foraging times and energy expense increase, while optimal diets may become more restricted. Optimal use of habitat patches also parallels the diversity and quantity of items in the diet within a patch. MacArthur and Pianka (1966) showed that the time spent for each item attained within suitable patches is an increasing function of the number and variety of patches within the range of that individual. As food density and availability increase, search times and energy expenditure decrease and patch use will be more restricted where food is dense. Hassel *et al.* (1976) illustrated that, in real environments, populations are often aggregated according to an uneven distribution of available forage or prey, resulting in an aggregation of individuals. The result is that because forage is more disparate and dispersed in larger patches, time-energy budgets are more vulnerable and larger patches tend to be used in a more specialised manner than smaller patches.

Competition has a similar effect: territories are both economical and physically defendable, such that as competition increases, patch use will shrink (Brown 1964). Otherwise, models of optimal foraging space suggest that the costs of territorial defence either improve or reduce overall fitness. For semi-territorial species like bears, if territory establishment, advertising, or monitoring are interrupted, it can result in occupancy by challengers and, thus, more energy may be lost and invested in defence. Ultimately, in addition to the bio-energetics of optimal foraging, the bio-economics of resource or territorial defence will play an important role in shaping an individual's foraging strategy (Brown and Orians 1970, Brown 1971, Schoener 1971).

McNab (1963) suggested that as body weight increases in mammals, there will be a corresponding increase in home range or territory size, which is at a rate proportional to body weight and metabolic rate. Species that require large home ranges are often hunters (omnivorous, carnivorous, insectivorous, frugivorous, or granivorous) with large body sizes and home ranges that are about four times larger than "croppers" (folivores) of the same body weight (McNab 1963). The energy requirements of these hunter taxa cannot support dense populations, because of the limited amount of food energy available within a given area. McNab (1963) suggests that carnivore densities average about 0.1 kg/ha, whereas the average density for folivores is about 6 kg/ha.

The daily energy exchange, rather than the basal energy expenditure, is most important for mammals. A large mammal uses more energy and needs a greater area to support its food energy needs. Because a primary determinant of home range size is an individual's metabolic rate, then adverse environmental conditions affecting food availability and density will influence home range size (McNab 1963) and, thus, an individual's movement patterns in the landscape. Differences in foraging or home range sizes *within* mammal species are related to variability in food productivity. Models show that frugivorous and carnivorous species tend to have larger home ranges where food availability is patchy (Schoener 1971), such as in the tropics. Thus, large carnivores or fauni-frugivores, such as sun bears, need to use their home ranges as efficiently as possible and will tend to diversify food sources when their ranges are restricted. Further, continuous feeders like bears can be severely impacted by forage loss, interruptions, or availability (Charnov *et al.* 1976).

As patch suitability declines, the amount of time, travel and range needed to optimise food gain increases with a proportional increase in energy expense. The loss of energy intake can be significant and often depends on the general availability of food and the need to search continuously (Charnov *et al.* 1976). If a food item becomes rare within a particular patch, then an imbalance will occur in the individual's time-energy budget and

optimal use of that patch will decline (MacArthur and Pianka 1966). In patches where food density is reduced, specialist species suffer and become vulnerable to competitive replacement.

To maximise efficiency in patches with resource depression (Charnov *et al.* 1976), the Marginal Value Theorem (Charnov 1976) predicts that exploitation of those patches should occur until the rate of gain within the patch decreases to the average across the organism's range (Charnov 1976, Krebs and Davies 1984). If travel time or distance between patches increase, the optimal time spent in a patch also increases in a linear fashion, i.e. the cost of moving is amplified and exploitation of the current resource is maximised (Charnov 1976, Krebs and Davies 1984). A more productive habitat would lead to a more restricted diet, where the variety and quantity of different food items will be less.

Where food supplies are patchy, an organism's visiting patterns are driven by resource depletion and renewal rates (Smith 1980). At a given level of consumption, food availability, locations, and renewal rates will then determine movement patterns and home range sizes (McNab 1963, MacArthur 1968, Smith 1980). The rate of return to a poor site then will be influenced by: (1) the risk of remaining in the poor patch, (2) the significance of forage interruption and loss of energy intake, (3) the risk of remaining in the new patch, (4) the risk of moving between the new and old (poor) patches, and (5) the loss per unit time by an interruption of other activities like courting, mating, nesting, territorial defence, and so on (Charnov *et al.* 1976). The consequences for feeding interruption are critical, particularly for mammal species like bears and primates with relatively long-term parental care and slow development times. For offspring of these species, malnutrition can increase mortality rates as well as higher risks of predation (Charnov *et al.* 1976, Schoener 1971).

MacArthur and Pianka (1966) illustrate that movement distances and obstacles will be part of the individual's overall foraging strategy. When fragmentation and patchiness increase, search time and energy expenditure also increase and optimal use of resources declines. Physiological needs, such as egg production or thermoregulation will add to feeding costs and create energy deficits. Ultimately, optimal foraging theory predicts that an organism proceeds through life gaining and expending energy to maximise its total reproductive output (Schoener 1971). Energy deficits will affect reproductive success, where the cost of foraging will reduce the time and energy needed for searching, finding, and succeeding as a fit mate. Thus, in a fragmented landscape, time and energy are used more for basic foraging needs (MacArthur and Pianka 1966), resulting in a direct proportional decline in reproductive success and fitness (Schoener 1971). When an individual encounters a permeable boundary, i.e. one that it perceives with low risk, it exercises a choice regarding potential costs of crossing the boundary *versus* the gains of acquiring new or better habitat (figure 3.6) (Wiens 1992, Augeri 1995). The costs and benefits include predation risk, physiological stress, foraging success, reproductive output and mating success, intra- and inter-specific competition, and resource availability (Wiens 1992). If there is a strong preference for the site or habitat type across that edge, animals may cross from the less preferred site, but would have difficulty doing so in reverse (Wiens 1992). Environmental factors across the boundary, such as exposure, temperature and humidity differentials, and so forth can induce physiological stress, which will factor into an organism's decision to stay or cross that boundary (Augeri 1995). Predation risk and forage availability rank high in the cost:benefit decision. Over time, when organisms perceive the potential costs as higher than benefits for crossing, it can create an imbalance of organisms on both sides of the boundary and can lead to an aggregation of individuals in the favoured patch (Wiens 1992).



Figure 3.6. Hypothesized changes in transfer rate between patches as a function of the degree of preference by the individual. The differential increases with increasing patch preference. Increasing preference also causes aggregation of organisms in selected patches. (Adapted from Wiens 1992).

When food density or availability is reduced, compression effects can influence foraging strategies and habitat use (MacArthur and Wilson 1967). Competition, environmental stochasticity, or anthropogenic factors, such as highly-contrasting edges and fragmentation, can force an organism to reduce its range or the variety of patches used, because some patches or movement between them will be less preferred or profitable (MacArthur and Pianka, 1966, MacArthur and Wilson 1967, Wiens 1992, 1997, Augeri 1995). Remaining forage availability will then influence a shift in diversity within patches used, often to secondary or tertiary types that are less nutritionally and energetically profitable (MacArthur and Wilson, 1967, Schoener 1971, Johns 1983, Johns and Skorupa 1987, Gilbert 1994, Lovejoy *et al.* 1986, Gilbert and Setz 2001).

What does this mean for bears? Ursidae, including sun bears, are "omnivorous" foragers with large ranges and variable movements that maximise food gain (Jonkel and Cowan 1970, Rogers 1976, 1987, Craighead *et al.* 1995, Powell *et al.* 1997). According to theoretical constructs, such species will search for food items simultaneously, such that:

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\frac{e}{t} = \frac{Potential \, Energy - Pursuit \, Costs - Handling \, and \, Eating \, Costs}{Pursuit \, Time + Handling \, and \, Eating \, Time}
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where e = energy, t = time, and digestion is assumed to be simultaneous with feeding (Schoener 1971). McNab (1963) suggested that available food is proportional to area used and that an organism occupies a home range that is not larger than the area needed to supply sufficient energy to maximise fitness. Where food density and availability vary in time and space, short-term energy demands may not be met and home range size will increase (Schoener 1971), as observed in different Ursidae (Jonkel and Cowan 1970, Rogers 1976, 1987, Craighead et al. 1995, Powell et al. 1997). To maximise fitness, most species need to minimise travelling time and energy expense between food items (MacArthur 1968), including bears (Rogers 1976, 1987, Craighead et al. 1995, Powell et al. 1997). In a patchy landscape, the degree of connectedness between patches (or food items) will ultimately affect the organism's fitness (Soulé 1980, Frankel and Soulé 1991). Scientific studies consistently demonstrate that bear fitness is directly related to nutritional health and stability. For a bear, this means the degree to which it can harvest food on a semi-consistent basis while moving along its foraging route, which can be as much as 20 hours/day (D.M. Augeri unpubl. data, C. Jonkel pers. comm.). Thus, because habitat fragmentation and highly contrasting edges in the landscape can reduce or block an orgnism's access to high-quality foods and habitat (Augeri 1995), including for bears (Augeri 1994, 2003, Craighead and Vyse 1996, Mattson et al. 1996, Merrill et al. 1999, Craighead et al. 2001, Larkin et al. 2004), this can directly and indirectly affect bear nutrition, reproductive success, population dynamics, and fitness (Rodgers 1976, Craighead et al. 1995, Craighead and Vyse 1996, Merrill et al. 1999, Servheen et al. 1999).

Food availability and diversity are two of the most prominent ecological factors influencing bear habitat use. Reduced food density, availability or access can influence bear health, movements, mating, recruitment, and population dynamics (Jonkel and Cowan 1970, Rogers 1976, 1987, Augeri 1994, Craighead *et al.* 1995, Powell *et al.* 1997, Servheen *et al.* 1999, Craighead WWF 2000, Larkin *et al.* 2004). For many bears, including sun bears, food diversity is particularly important for maintaining adequate nutrition levels. Because preferred plant and animal foods fluctuate across time and space, bears tend to be highly efficient omnivores, selectively maximising nutritional requirements through learned behaviour and traditional movement patterns to proven food resources.

Fruit availability and diversity are highly important for sun bear nutritional stability. When fruit availability is low, species like sun bears with a predominantly frugivorous diet depend on other food sources, especially in small forests where key foods may be less diverse or abundant (Augeri 2003, Meijaard *et al.* 2005, S. Wulffraat pers.comm.). In contrast, large contiguous primary forests sustain more diverse and abundant forage across the landscape. For bear species like sun bears with co-evolved adaptations to specific habitat and forage types, altering the density and abundance of food and other resources can change the bear's movement dynamics and occupancy across the landscape (Mattson *et al.* 1987, McLellan and Shacklton 1988, Mattson *et al.* 1996, Merrill *et al.* 1999, Boyce 2000, Augeri, 1994, 2000, 2003, Meijaard *et al.* 2005).

3.3 <u>Risk-Disturbance Hypothesis</u>

Anthropogenic disturbance has been proposed by several authors as explicitly analogous to predation risk (Gill *et al.* 1996, 2001, Gill and Southerland 2000, Frid and Dill 2002). Known as the risk-disturbance hypothesis, the same cost-benefit principles proposed by predation theory and, in some cases foraging theory, are used to predict that responses by disturbed animals will parallel proximate changes in disturbance stimuli. Essentially, an animal's response will be stronger when perceived risk increases (Frid and Dill 2002). The indirect effects induce survival and reproduction trade-offs with energy intake, perceived risk, and subsequent habitat use. Consequent density-dependent processes are affected by food distribution and disturbance stimuli, which then determine population dynamics and/or habitat changes (Gill and Sutherland 2000). Optimal-foraging theory predicts that animals will optimise their energy budgets relative to these trade-offs, but investment in anti-predator behaviour will divert time and energy away from fitness-enhancing activities. In many cases, non-lethal human activities or disturbance may induce similar responses and effects (Gill *et al.* 1996, 2001, Gill and Sutherland 2000, Frid and Dill 2002).

Disturbance stimuli can indirectly affect overall population dynamics by causing individuals to divert disproportionate amounts of time and energy away from food intake (Frid and Dill 2002). Frid and Dill (2002) summarise disturbance-risk predictions relative to habitat use, such that (1) persistent and intense disturbance stimuli will cause habitat shifts at the cost of reduced access to resources and (2) habitat shifts will not occur if alternative sites are lower in quality or are too distant, for which the costs of changing sites will outweigh the benefits of moving.

Some individuals exposed to disturbance stimuli may not have the ability, or will not attempt the perceived risk, to shift sites. Consequently, the effects of insularity will increase. For animals that cannot move from disturbed habitats, activity budgets will be disrupted and competition will apply more pressure *via* crowding in smaller remaining patches (Gill *et al.* 2001). Where disturbed patches are sub-optimal, increased energetic costs associated with foraging, competition, increased predation risk, and disturbance avoidance can further reduce effective habitat quality. As such, body condition deteriorates, parasite loads increase, physiological stress can rise, and survival and reproductive success are compromised (Frid and Dill 2002). These effects can be exacerbated during periods of environmental stress or stochastic events like drought (White 1983, Frid and Dill 2002). Where disturbance risk induces individuals to avoid important foraging areas or more optimal habitat, higher energetic costs and density-dependent processes will affect demography, population, and community level dynamics (Gill and Sutherland 2000, Frid and Dill 2002).

According to Gill *et al.* (1996), four components of data are required to quantify disturbance risk: (1) the amount of a defined resource/unit area, (2) the proportion of this resource that is exploited, (3) the total number of individuals supported by this resource, and (4) some measure of disturbance. This hypothesis differs from other studies of disturbance because it assesses the cost/benefit that animals face due to the rate of disturbance relative to the amount of available resources. A critical factor is if disturbance negatively affects population size with three primary assumptions: (1) animals have equal access to habitats and resources, (2) individual tolerances are constant, and (3) the threshold biomass is a minimum.

The Risk-Disturbance hypothesis can be applied to a variety of species and disturbance types, primarily because the effects of disturbance are examined as a trade-off in resource use by individuals and populations in response to the disturbance(s) (Gill *et al.* 1996, 2001). Further, it clarifies the effects of disturbance on population distribution and quantifies such effects relative to population size.

Sun bears may be influenced by risk-disturbance effects, but it is important to determine to what degree avoidance behaviour affects survival and fitness. Gill *et al.* (1996) suggest that the species most likely to be negatively affected by disturbance have reduced or no access to alternative resources and suffer reduced survival and reproductive success. Wong (2002) found that the health, body condition, and survival of sun bears in Danum Valley, Sabah, which is surrounded by ca. 1 million ha of logging concessions, were severely compromised by low forage availability. Meijaard *et al.* (2005) suggest this was probably due to the synergistic interaction of logging disturbance and the El Niño Southern Oscillation (ENSO) event of 1997-1998.

Extensive logging can also stimulate micro- and macro-climate changes and exacerbate the stochastic effects of events like ENSO, inducing ecological changes in temperature, moisture, evapo-transpiration, light penetration, wind turbulence, and so forth, all of which affect plant biology and reduce fruit and seed productivities (Whitmore 1997, Lovejoy *et al.* 1986, MacKinnon *et al.* 1996, Bierregaard *et al.* 2001, Meijaard *et al.* 2005). It is possible that, due to logging across the more than 1 million ha bordering the Danum Valley protected area, sun bears either could not access more productive areas or were forced to change sites to less suitable habitat with lower and less diverse productivity. Normua *et al.* (2003, 2004) found that sun bears near an oil palm estate in Sabah spent 88% of their time in interior forests > 1 km away and 100% of any time near the plantation was at night when no people were present. Consequently, the habitat use of these bears may be categorised by hypothesis one above, in which disturbance stimuli will influence risk

behaviour of changing habitats at the expense of reduced access to resources (Frid and Dill 2002).

This potential risk behaviour parallels the majority of species and studies reviewed by Frid and Dill (2002). In another example, White *et al* (1999) observed that disturbance stimuli probably induced grizzly bears to reduce their energy intake of an important highcaloric food resource (army cutworm moths, *Euxoa auxiliaries*) by an average of 12 kcal/min when disturbed by hikers. These bears were forced to spend more time and energy in flight response or aggressive defence toward the human intruders. As a result, White *et al.* (1999) predicted that the health and reproductive output of the bears would deteriorate if net energy gain continued to decline. Bear cases correspond with most mammals in that, if such disturbance stimuli persist in duration and intensity during periods of high environmental stress, the health and fitness of the animals could deteriorate, eventually causing subpopulation declines that can impact the persistence of the overall population (Frid and Dill 2002).

3.4 Perturbation-Stress Hypothesis

Basic physiological requirements mandate that warm-blooded species must be constantly active in a landscape to acquire resources. Metapopulation theory suggests that the size, distribution, and access to suitable habitats either enable or limit an individual to reproduce successfully and contribute genes to future generations (fitness) (Hanski and Gilpin 1997) (*see* proceeding section). If access to resources is limited or blocked by habitat disturbance or human activities, this can create fragmented or isolated populations with potential risks to their persistence and evolutionary potential (Soulé 1980, Frankel and Soulé 1992), including bears (Craighead *et al.* 1995, Craighead and Vyse 1996, Waits *et al.* 1999).

Disturbance is relative and variable depending on its intensity, scale, individual tolerances, and the particular species affected (Augeri 1995, Laidlaw 2000). Under the same conditions, some species or individuals may be intolerant of a particular disturbance, while others will show little effect. Stress is defined as the disruption of an organism's homeostasis (Moberg 2000) and individual tolerance will determine the level of stress that organism can endure. Stress at an individual level is often manifest in physiological imbalances and behavioural changes due to resource depletion, energy expense, isolation, and social system break-downs. Many species, including carnivores and primates, will have amplified levels of parasites and infectious diseases that will affect their survivability, persistence, and fitness (Harris and Scheck 1991, Gilbert and Setz 2001). Proximate effects are most often manifest in behaviour changes like fleeing, cessation of foraging, or altering reproductive behaviour (MacArthur et al. 1982, Knight and Cole 1991, Taylor and Knight 2003). This can lead to energetic losses from excess "flight" responses, decreased foraging times, and increased stress levels at the expense of food resources needed for growth, survival and reproduction (Geist 1978, Taylor and Knight 2003). Disturbance and/or human activity can also induce many species to avoid portions of their normal range (Hamr 1988), which can result in reduced forage availability and subsequent energy deficits, reproductive failures, and survival (Miller et al. 2001, Taylor and Knight 2003). Thus, displacement from otherwise suitable habitat could result in negative energetic and behavioural consequences (MacArthur et al. 1982, Miller et al. 2001), which can increase stress levels (Taylor and Knight 2003) and affect both immediate and long-term survival (Geist 1978).

When various individuals are affected by stress within a population, there can then be a direct proportional influence on that population's persistence trajectory (Soulé and Wilcox 1980, Hanski and Gilpin 1997, Young and Clarke 2000). Terborgh and Winter (1980) discuss the more important causes of extinction across taxa due to fragmentation, for
which loss of forage, mutualisms, and other ecological relationships at an individual level are critical to local population persistence:

- (1) Primary Causes: Stochastic extinction due to reductions in population size; found mainly in large or nomadic species along with habitat specialists due to:
 - (a) Fragmentation.
 - (b) Negative population growth.
 - (c) Species dependent on irregular or patchy resources.
- (2) Secondary Causes: Ecological imbalances resulting from fragmentation and negative population growth, due to:
 - (a) Alteration of interaction webs, particularly predator-prey and pollinator-disperser relationships.
 - (b) Loss of forage, prey species, and mutualisms, etc. due to the combined effects of all of the above.

Physiological stresses can affect bears (Cattet *et al.* 2003, van der Ohe *et al.* 2004, Owen *et al.* 2004, Wasser *et al.* 2004). Reduced food density, availability or access can induce stress and influence bear health, movements, mating, recruitment, and population dynamics (Jonkel and Cowan 1970, Rogers 1976, 1987, Craighead *et al.* 1995, Powell *et al.* 1997, Wasser *et al.* 2004). Wong (2002) observed significant mortality rates (33 – 66%) from poor nutrition in captured sun bears due to low forage availability in Danum Valley, Borneo. Craighead *et al.* (1995) showed over a 33-year study of the grizzly bear population in the Yellowstone Ecosystem that nutrition and access to suitable foods have both proximate and long-term effects on individual bears and, thus, recruitment and the persistence of the overall population. Harris (1984) showed this relationship at landscape scales across taxa and ecosystems and many other studies provide sound empirical evidence and theoretical foundations for these types of stresses on population persistence (*see* Soulé and Wilcox 1980, Frankel and Soulé 1981, Lovejoy *et al.* 1986, Beirreggaard *et al.* 2001, Hanski and Gilpin 1997, Caro 1998, Hanski 1999, Young and Clarke 2000).

Based on species-area relationships ($S = cA^z$), island biogeography theory demonstrates a direct linear relationship between extinction rates and area, which holds true across a variety of species and taxa (*see* section 3.1) (MacArthur and Wilson 1967, Simberloff and Wilson 1969, Diamond 1975, Wilcox 1980, Harris 1984). Wilcox (1980) demonstrated this relationship well by using the current diversity of land mammal fauna of the Malay Peninsula as a benchmark to compare with the Sunda Islands prior to their isolation (figure 3.7).



Figure 3.7. Relationship between the number of species of mammals and land area of the Malaysian mainland (upper line) and the Sunda Islands (lower line). The upper line (S = $15.4 \text{ A}^{.17}$) approximates the species-area relationship of the Sunda Shelf prior to fragmentation by rising sea levels at the end of the Pleistocene. The lower line (S = $1.8 \text{ A}^{.30}$) shows the current diversity and differs as a result of fragmentation and the collapse of isolated faunas. Note that the most diverse fauna are located on the largest land masses in the following order: (1) Borneo, (2) Sumatra, and (3) Malay Peninsula compared to smaller reserves/islands (4) Krau Game Reserve, (5) Bali, (6) Pini, and (7) Bangkaru (adapted from Wilcox 1980).

When considering persistence curves, however, each foraging class might respond differently to the same disturbance effect. Figure 3.8 shows a hypothesised relationship between population persistence and habitat disturbance. Conceptually, as the level or intensity of disturbance increases, the persistence of a particular foraging class will reflect a general linear or curvilinear response over time. As shown, more sensitive species, such as



Figure 3.8. Hypothesized relationship between population persistence and habitat disturbance. Taxa and individuals within a species will respond differently to perturbations. While the flexibility of generalists may enable such organisms to adapt to some disturbances and occupy a patch at various densities around the 95% persistence level, habitat specialists and obligates will decline more rapidly. Once a critical threshold is reached, these taxa may not recover.

specialists and obligates, will drop-off more rapidly then generalists or pioneers. The latter group may hover around the 95% persistence level, where some pioneer or generalist species may benefit from particular types of disturbances like edges, while others may be affected, but could adapt to changing conditions and switch to other resources.

Sensitive species will decline at a more rapid and perhaps accelerating rate if disturbance is not abated. As the rate of decline and disturbance continue, that population may reach a critical threshold beyond which the probability for recovery is minimal. In his discussion of non-equilibrium insular biogeography, Brown (1971) demonstrated this relationship empirically, where the persistence of different taxa and foraging classes (generalists, specialists, etc.) was influenced by isolation and differences in food density. Wilcox (1980) also discusses the differences in taxa in response to isolation. In particular, mammals are expected to decline more rapidly than birds, reptiles or amphibians. In general, physiological stress on individual organisms and demographic or genetic stresses at the population level are common denominators in these situations.

Several theoretical models have been used to test object stress (Weilbull 1949, 1951, Johnson 1964) that parallel species-area relationships and island biogeographic models (MacArthur and Wilson 1967, Simberloff and Abele 1982, Diamond 1975, Harris 1984). Although there has been considerable debate in both fields, it is worth exploring these parallels to examine the potential ecological implications for conservation biology applications.

The Weibull Inverse Power Law model (or relationship) is commonly used in engineering to examine longevity relative to stress (Weibull 1949, 1951, Johnson 1964). The general concept of stress tolerance is adapted here to examine potential perturbation stress on organisms and subsequent population persistence. The basic model is represented by:

$$L(V) = \frac{1}{KV^n}$$

where, *L* represents a quantifiable life measure, such as mean longevity, characteristic life, median life, etc., *V* represents the stress level, *K* is one of the model parameters (e.g. slope) to be determined (K > 0), and *n* in the inverse power relationship is a measure of the effect of the stress on longevity. As the absolute value of *n* increases the greater the effect of the stress on the object. Negative values of *n* indicate an increasing life with increasing stress. An absolute value of *n* approaching zero indicates a small effect of the stress on the life, with no

effect (constant life with stress) when n = 0. Figure 3.9 demonstrates this relationship at various stress levels.



Figure 3.9. The basic inverse power law relationship on linear scales at different life characteristic levels, including a Weibull life distribution, where n = effect of stress. The upper line shows the effect at 10% and the lower line at 90%. (Adapted from Weibull 1949).

In most practical applications, life is a function of more than one or two variables that exert stress. Thus, when a situation involves multiple accelerating stresses, a general multivariable relationship is needed (Reliasoft 1997). Such a relationship is the general log-linear relationship, which describes a life characteristic as a function of a vector of *n* stresses, or $\underline{X} = (X_1, X_2, X_3...)$. Mathematically the model is given below, where ${}^{\alpha}j$ are model parameters and \underline{X} is a vector of *n* stresses.

$$L(\underline{X}) = e^{\alpha + \sum_{j=1}^{n} \alpha_j X_j}$$

The Proportional Hazards model was developed in order to estimate the effects of different covariates influencing the "times-to-failure" of a system (Reliasoft 1997). According to the model, life failure rate is affected not only by time, but also by the covariates under which it functions. The instantaneous failure rate (or hazard rate) is given below, where, f(t) is the probability density function and R(t) is the reliability function.

$$\lambda(t) = \frac{f(t)}{R(t)}$$

The proportional hazards model assumes that longevity is the product of an arbitrary and unspecified baseline failure rate, $\lambda_{0}(t)$, which is a function of time and a positive function $g(x, \underline{A})$, independent of time, that incorporates the effects of covariates. In the situation where failure rate is dependent on both time and other covariates, the model must be modified to be a function of time and of the time-independent stress-related covariates.

The basis of the inverse-power concept can be applied to biological systems, individuals, populations, and species. Wiens (1997) shows that the effects of isolation are minimal when suitable habitat coverage is high, but, according to percolation theory, the effects increase sharply as connectivity decreases (figure 3.10), raising stress levels (Wiens 1992). Individual vagility can shift this threshold relative to the degree of isolation and available suitable habitat. As stress increases, individual and local extinction rates then reduce the effective population size in an area (Soulé 1980, Harris 1984, Frankel and Soulé 1992, Whitlock and Barton 1996, Hanski and Gilpin 1997). How this will influence the long-term persistence of the population at that site and potentially across its range is illustrated in figure 3.11.



Figure 3.10. Hypothesised relationship between the proportion of suitable habitat in a landscape and the relative importance of habitat loss and patch isolation to individual movement and population dynamics. Here, the effects of isolation are minimal when suitable habitat coverage is high, but according to percolation theory, the effects increase sharply as connectivity decreases. Individual vagility will shift this threshold relative to the degree of isolation and available suitable habitat. (Adapted from Wiens 1997).

When examining the slope of stress in the inverse power curve in figure 3.9, it clearly parallels these relationships, as well as that between the exponent Z value in the species-area equation $S = cA^z$ proposed by MacAurther and Wilson (1967), and the area necessary for increasing the number of species (Harris 1984) (*see* section 3.1). Brown

(1971) and others also demonstrated similar responses by species exposed to isolation. Conceptually, then, when applying the inverse-power relationship of stress to the persistence of species with semi-obligate behaviour, site or territorial affinity, or sensitivity to some form of disturbance, the site occupancy slope of those species might exhibit the same functional response as that of longevity to stress.



Figure 3.11. Increasing local extinction rates reduce effective population size of the species in a patch; N = 50, k = 2, and m = 0.1. (Adapted Whitlock and Barton 1996).

Defined here as the Perturbation-Stress Hypothesis, individuals may first respond gradually to disturbance, with a slope function similar to a minor or progressively-increasing perturbation (figure 3.12). In a disturbed system, as food and other resources (including mates) are depleted, social systems deteriorate, and home ranges are reduced, then more energy is spent with decreasing benefit in return. This can induce physiological stress (Moberg 2000), which for bears can raise glucocortocoid, progesterone, and other stress hormone levels, induce risk-response behaviour, and alter normal behaviour and movement patterns (White *et al.* 1999, Cattet *et al.* 2003, van der Ohe *et al.* 2004, Owen *et al.* 2004, Wasser *et al.* 2004). This has been shown in a variety of other species (Frid and Dill 2002), including wolves (Creel *et al.* 2002), elk (Millsangh *et al.* 2001, Creel *et al.* 2002), elephants (Foley *et al.* 2001), raptors (Delaney *et al.* 1999, Tempel and Gutierrez 2003), and salamanders (Newcomb Homan *et al.* 2003).



Figure 3.12. Perturbation-Stress Hypothesis. In a disturbed system, as food and other resources are depleted, more energy is spent with decreasing benefit in return, inducing physiological stress on individual animals. When sensitive species are exposed to prolonged and/or increasing levels of moderate to high stress, they can reach a critical threshold much sooner and individual survival and reproductive success will decline. The population's functional response may be an accelerated decline beyond which persistence at that site may not be possible.

Figure 3.12 shows the hypothetical relationship that when some obligate, specialised, or sensitive species are exposed to prolonged and/or increasing levels of moderate to high stress caused by perturbation, they may reach a critical threshold much sooner. At that point, individual survival and reproductive success will decline. If this trend persists across time and generations, the population's functional response may be a sharp and accelerated decline, beyond which persistence at that site may not be possible (figure 3.12). Depending on the size, distribution and connectivity of the metapopulation, local losses could lead to a more rapid extinction of the sub-population or overall population (Soulé 1980, Harris 1984, Frankel and Soulé 1992, Hanski and Gilpin 1997). This relationship appears to be common in many species (Frid and Dill 2002), but will clearly depend on the tolerance level of each individual, the population's fecundity pattern (e.g. r or k selection), and particular demographic and ecological conditions.

Wasser *et al.* (2004) demonstrated in an extensive field study of brown bears (*U. arctos horribilis*) in Alberta, Canada that concentrations of faecal cortisol and progesterone metabolites were influenced by habitat disturbance and human activity. Physiologic stress was lower, while female reproductive productivity was highest in areas with less habitat disturbance and human use. In a different study of brown bear faecal glucocorticoids levels in Alaska, van der Ohe *et al.* (2004) discovered that a change in diet explained the most variation in glucocorticoid concentrations. Further, the interaction between diet and time of year could be explained by stress, where glucocorticoid concentrations increased over the course of the season depending on diet type and time proximity to pre-denning (van der Ohe

et al. 2004). Thus, under natural conditions forage changes can induce physiological stress responses in bears, but because disturbance can disrupt access and change the composition and abundance of available food items, disturbance can replicate such stochastic events and induce physiological stress. Creel *et al.* (2002) noted that the hypothalamic-pituitary-adrenal axis increases secretion of glucocorticoids as a response to physiological or behavioural stressors in mammals. While these responses are "adaptive" over short periods, chronic elevation of glucocorticoid concentrations can produce various diseases. The latter include reproductive suppression, muscle wasting, immune suppression, and ulcers, all of which will contribute to reduced survival and fitness, particularly as the stressor increases in severity or duration (Creel *et al.* 2002).

Increases in cortisol with declining nutritional intake and health have been found in a variety of mammals (Creel et al. 2002). If disturbance stressors occur during periods of physiological stress, more long-lasting physiological imbalances, declining health, and low reproductive output could impact those individuals. In an experiment with captive giant pandas (Ailuropoda melanoleuca) Owen et al. (2004) found that elevated and persistent anthropogenic noise levels significantly increased behavioural agitation in both panda genders and increased glucocorticoid levels in females. For wolves and elk in three national parks in North America, there were definite physiological stress reactions seen in elevated faecal-glucocorticoid concentrations when responding to snowmobiles (Creel et al. 2002) and other human activities, particularly increased road and foot traffic (Millspaugh et al. Free-ranging African elephants exhibited increased faecal cortisol metabolite 2001). concentrations during periods of drought, food shortage, and social disruption. Delaney et al. (1999) and Tempal and Gutiérrez (2003) demonstrated that several types of human disturbances can negatively impact Mexican spotted owls (Strix occidentalis lucida) and other raptors, particularly from proximate human activity and noise generated from chainsaws, which induced increased behavioral (e.g. flushing, lower reproductive success) and physiological (faecal-corticosterone concentrations) stress responses. Frid and Dill (2002) discuss predation risk theory (see section 3.4 on Risk-Disturbance Hypothesis) relative to anthropogenic disturbance, where disturbance stimuli are analogous to predation risk and can affect habitat use, behaviour, survival, and reproduction through perceived risk and energy balance.

In general, physiological and behavioral stress responses in sun bears can be exacerbated by disturbance, particularly if an individual is already in a physiologically stressed state due to poor diet, unsuitable or insecure habitat (Augeri 2003, Meijaard *et al.* 2005), or environmentally-stochastic conditions, such as drought (Fredriksson 2005),

temperature increases/decreases, and so forth. During such periods, prolonged or increased human disturbance and activity can result in significant negative impacts on the individual, ranging from declining health to reduced survival, reproduction, and fitness. There is sufficient evidence to suggest, therefore, that the population and demographic consequences of habitat fragmentation, patch isolation, insularity, and associated human disturbance can be exacerbated by increased stress levels in remaining sun bears, leading to a more rapid decline in longevity, fitness, and persistence. The geometry of landscape structure can influence species persistence and, thereby, ecological and evolutionary processes. Species, and even ecological processes, are ephemeral, especially on a local level, and are dependent on the degree to which increased isolation and loss of suitable habitat affect within-patch dynamics (e.g. density, demography, competition, birth rates, mortality) and between-patch processes, such as dispersal, colonisation, and gene exchange (Thrall *et al.* 2000). Fragmentation effects, such as isolation, insularity, loss of habitat, and edge effects, can independently and synergistically influence the availability and abundance of critical resources, as well as competitive and density-dependent interactions for those resources. Over time, this can lead to negative effects on individual survival rates, reproductive success, and fitness (*reviews in* Hanski and Gilpin 1997, Young and Clarke 2001).

A key component of survival for most animals is the ability to access suitable habitat, resources, mates, cover, security, and territory across the landscape. The vulnerability of individual populations in isolated patches can be significant. Insularity, forage loss, and habitat degradation, among other factors, can affect individual survival rates in isolated patches. In addition to these and other effects of fragmentation, environmentally-stochastic events (e.g. drought, fire, disease) can independently and synergistically interact with fragmentation and lead to extinctions beyond local patches (Thrall *et al.* 2000, Laurance and Williamson 2001, Meijaard *et al.* 2005). Consequently, species and community persistence depend on (1) unrestricted movement and dispersal of individuals to enhance their survival and genetic and demographic diversities (Hubbell 2001) and (2) sustaining access to critical resources and habitat on a regional level for recruiting new individuals across multiple generations.

Much of the remaining forest areas in South-East Asia are fragments surrounded by agriculture, clear-cuts, and development. These remaining areas and the species therein are not immune to disturbances (Wilson and Wilson 1975, Augeri 1991, 2003, Whitmore 1997, Laurance and Bierregaard 1997, Laidlaw 2000, Cuaron, 2000, Laurance *et al.* 2001, Bierregaard *et al.* 2001, Meijaard *et al.* 2005). The conversion of forests can subdivide animal populations and subject them to deleterious environmental, demographic, and genetic effects (Saunders *et al.* 1991, Augeri 1994, 1995, Hanski and Gilpin 1997). Isolated populations in a fragmented landscape can lead to metapopulation dynamics (Hanski and Gilpin 1991), including for bears where restricted movement among geographically-isolated sub-populations can result in either local extinctions within isolated patches (Augeri 1994, Craighead and Vyse 1996, Murrow 2001, Larkin *et al.* 2004) and/or complete population

A metapopulation is defined as a collection of partially- or fully-independent subpopulations existing in patches of habitat geographically separated by unsuitable areas (Levins 1969, 1970, Hanski and Thomas 1994, Hanski and Gilpin 1997). Long-term persistence of the metapopulation depends on the stability and relatively independent dynamics of its sub-populations along with an appropriate balance between extinctions and colonisations of new patch populations by occasional dispersal events (Levins 1969, 1970, Hanski and Thomas 1994, Doak and Mills 1994, Hanski and Gilpin 1997). Although this theory assumes that dispersal is occasional or perhaps infrequent, the importance of dispersal and colonisation for structuring populations and communities is critical to long-term persistence (Hubbell 2001).

Metapopulation models incorporate the basic concepts of island biogeography theory, but predict non-linear effects of habitat loss, such that populations will decline or entire species will become extinct when the quantity of remnant habitat decreases below an acute threshold fixed by those species' dispersal and extinction characteristics. By linking and providing more habitats with corridors, extinction probabilities are reduced by aiding dispersal, colonisations, demographic stability, and gene exchange (Harrison and Bruna 1999). In most metapopulation models, no true "mainland" or source population exists; rather "mainland-island" metapopulation models assume that a core population may exist in a large habitat patch where extinction probabilities are very low (Hanski 1991, 1996). Colonisations result from inter-patch dispersal events, where patch size and heterogeneity, isolation, and evolutionary changes in the species' colonisation abilities are factors (Hanski 1991).

In general, metapopulation models are considered either spatially implicit or explicit. Levins (1969, 1970) developed one of the first patch models, which is spatially implicit, based on the concept that species can exist in a regional network of habitat patches with independent probabilities of extinction. This model formed the foundation of the theory of metapopulation dynamics and was proposed by Levin as:

$$\frac{dP}{dt} = cP(1-P) - eP$$

where the rate of change, P, in metapopulation size over time, t, is a function of the rate of local extinction, e, and the rate of colonisation, c. The rate of colonisation is assumed to be proportional to the fraction of currently-occupied patches, denoted by p, and the fraction of

empty patches as 1 - P. This model has been used to predict metapopulation dynamics of single species, predator-prey interactions, and competitive relationships (Hanski and Gyllenberg 1993, Thrall *et al.* 2000). Several problems exist with the model; most notably whether local patch populations are unstable. Consequently, there cannot be an accurate prediction if the metapopulation is actually undergoing extinction processes (Doak and Mills 1994).

Sub-populations are connected by dynamic processes among patches, which are often affected by within-patch demographic and genetic processes (Thrall *et al.* 2001). Thus, density-dependent "structured" models incorporate the effects of dispersal and patch population dynamics on growth rates and extinction (Gyllenburg and Hanski 1992). These metapopulation models assume that all patch populations are equally connected, which is often *not* the case. Nevertheless, structured models offer spatial variation in patch size and consider the fact that some patches may remain empty despite frequent migrations among patches. The latter is realistic in fragmented landscapes, depending on the species, its spatial requirements, patch size, the degree of its isolation, and the suitability of habitat within the patch and in the surrounding matrix to access that patch.

Spatially-realistic and spatially-explicit models are more applicable to conservation biology questions and incorporate the MacArthur and Wilson (1963, 1967) island biogeography equation of a mainland-island concept for a single species (Hanski 1993). A strong advantage of these models is that relatively simple non-linear regression modelling can be used to fit empirically-derived presence-absence data from habitat patches with known areas and distances of isolation (Hanski 1993, 1996). Essentially, if only small fragments exist, the long-term persistence of a population is dependent on regional processes, but density-dependent dynamics within and between patches remain important intrinsic effects on this process (Hanski 1996). These models assume that a local patch population will primarily interact with its closest neighbouring population, which will help maintain persistence of the metapopulation. Various landscape or anthropogenic features, however, may affect the balance between local colonisations and extinctions, where the availability and abundance of forage and other primary resources, demographic ratios, population densities and so forth will influence within-patch dynamics and the relative degree of isolation and connectivity among patches.

Bear movement between patches is vital, particularly relative to inter-patch distances where local sub-populations will mix and act as a single large population (Craighead and Vyse 1996, Boyce 2000, Murrow 2001, Boyce *et al.* 2001, Larkin *et al.* 2004). Wiens (1997) noted that, in a landscape with decreasing proportions of available suitable habitat, continued

habitat loss results in rapidly-increasing distances between patches and greater isolation effects. If movement between patches is restricted due to barriers from development, roads, or inhospitable terrain, the recolonisation of isolated sub-populations that are in decline or extinct can lead to extinction of the entire metapopulation (Wiens 1992, 1996, Hanski and Gilpin 1997). Even for large vagile species like bears, movement restrictions and access to critical resources can be deleterious to the population (Craighead and Vyse 1996, Noss *et al.* 1996, Merril *et al.* 1999, Waits *et al.* 1999, Boyce 2000, Bader 2000, Murrow 2001, Maher *et al.* 2003, Larkin *et al.* 2004).

When local extinction and recolonisation rates are dependent on patch size and isolation, as explained in classic metapopulation theory, the occupancy of American black bear (*U. americanus*) habitat patches in the southern Appalachian mountains and Florida can be explained (Murrow 2001, Larkin *et al.* 2004). Murrow (2001) tested this hypothesis using more than 10,000 black bear radio-telemetry locations across three southern U.S. states to define habitat patches at different spatial scales and resolutions. Using a spatially-explicit metapopulation model and non-linear regression, Murrow showed that, as patch area increased, the probability of its occupancy by black bears increased, but isolation was the most significant barrier to the long-term persistence of these fragmented bear populations.

Even without isolation, the addition of newly-created edge can significantly affect individual, population, and community-level dynamics in remaining forest areas (Augeri 1994, 1995, Wiens 1997, Whitmore 1997, Laurance *et al.* 2001, 2002), including for sun bears throughout their fragmented range (Santiapillai and Santiapillai 1996, Servheen 1999a, Servheen *et al.* 1999, Craighead 2000, Whitten *et al.* 2000, Augeri 2003, Meijaard *et al.* 2005). For example, physical and biotic edge effects can impact flora and fauna several hundred metres inside a forest (Loveyoy *et al.* 1986, Chen *et al.* 1992, Wiens 1992, Augeri 1995, Laurance *et al.* 2001, 2002, Bierregaard *et al.* 2001). Depending on the patch shape, such impacts can create the effect that even forest fragments as large as 10,000 hectares are virtually all edge by substantially reducing the area:edge ratio (Wiens 1989, 1992, Augeri 1995, Harrison and Bruna 1999, Laidlaw 2000, Bierregaard *et al.* 2001). Consequently, a high proportion of individuals and species within that patch are affected (Lovejoy *et al.* 1986, Wiens 1992, Augeri 1995, Laurance *et al.* 2001, 2002, Bierregaard *et al.* 2001).

Although different disturbance types may appear similar in their effects, silvicultural alterations of edge are often distinct from those formed by fire, wind, or by various biophysical associations (Lovejoy *et al.* 1986, Forman 1987, Augeri 1995). Depending on the scale, intensity, and type of a disturbance, the hierarchical structure of edges in that landscape may be simplified (Augeri 1995). As a result, creating homogeneous sharp edges

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across landscapes can potentially decrease habitat connectivity (Noss 1991, Forman and Moore 1992, Augeri 1995) and, therefore, the flow of organisms (Ambuel and Temple 1983, Morris 1988, Wiens 1989, 1992), propagules (Slayter and Noble 1992, Chen *et al.* 1992, Kay *et al.* 1994), and genes (Gilpin and Soulé 1986) through the landscape. This includes movement patterns and gene flow for highly-mobile species like bears (Craighead and Vyse 1995, Noss *et al.* 1996, Waits *et al.* 1999, Merrill *et al.* 1999, Boyce 2000).

Disturbance in either continuous tropical forests or temperate forests can shift plant types, ages, patterns, and assemblies (Lovejoy *et al.* 1986, Bierregaard *et al.* 2001, Forman 1987). Accordingly, the dynamic effects of edge and landscape mosaic changes can alter faunal assembly (Merriam and Wegner 1992, Johnson *et al.* 1992) on a variety of spatial and temporal scales (Harris 1984, Lord and Norton 1990, Collins and Glenn 1991, Harris and Silva-Lopez 1992, Augeri 1995). Augeri (1995) demonstrated that edges differ inherently within a landscape and their effects are relative to each plant and animal species, as well as to individual organisms. These influences can affect habitat connectivity (Hansson 1991, Noss 1991) and, thereby, potential biotic and genetic flows in the landscape (Wiens 1989, Gosz 1991, Gardner *et al.* 1992, Augeri 1995).

For mobile species, such as sun bears with co-evolved adaptations to specific habitat types, changing continuous forests into abrupt, sharply-contrasting edges can change the bear's movement dynamics through the landscape (Mattson *et al.* 1987, McLellan and Shacklton 1988, Augeri 1994, 2000, Mattson *et al.* 1996, Merrill *et al.* 1999, Boyce 2000, Augeri 2003, Meijaard *et al.* 2005). Consequently, the structure and dynamics of sun bear sub-populations can shift. Lovejoy *et al.* (1986), Laurance *et al.* (2001, 2002), and Bierregaard *et al.* (2001) demonstrated that even micro-site alterations of Amazonian tropical forests by edge generation can result in community structure and species changes across broad spatial and temporal scales, either immediately or over several generations. This can affect individual organisms and their population persistence through a series of feedback loops. Meijaard *et al.* (2005), Laidlaw (2000) and Augeri (2003) came to similar conclusions for a wide variety of species on Borneo and Peninsular Malaysia, including sun bears. Given the sun bear's diverse ecological interactions and co-evolved adaptations, such community-wide effects can potentially impact the bear's population dynamics over the long-term.

Effects of habitat loss on the spatial distributions, isolation, and between-patch interactions of flora and fauna assemblages in a landscape may depend on organism biology, but sun bear movements across edges and inhospitable habitat to access critical resources may be constrained ultimately by the degree of fragmentation and edge (Stamps *et al.* 1987,

Buechner 1987, Mattson *et al.* 1987, McLellan and Shacklton 1988, Johnson *et al.* 1992b, Wiens 1992, Mattson *et al.* 1996, Augeri 1994, 1995). Habitat conversions that do not account for the cumulative effects of individual sites across wider temporal and spatial scales can affect the ecology, population dynamics, fitness, and evolutionary potential of bears (Mattson *et al.* 1987, McLellan and Shacklton 1988, Augeri 1994, 1995, Noss *et al.* 1996, Mattson *et al.* 1996, Craighead and Vyse 1996, Craighead *et al.* 1998, Merrill *et al.* 1999). Such populations, as well as species diversity and the richness of the landscape community, may eventually exhibit declines (MacArthur 1972, Whittaker 1977, Glasser 1982, Gilpin and Soulé 1986). Thus, in a landscape mosaic, inter-patch movements are a complex function of boundary permeabilities, landscape geometry and structure, species biology, and inter- and intra-patch dynamics (Augeri, 1995, Crooks 2002) like bears are affected (Augeri 1994, Noss *et al.* 1996, Merrill *et al.* 1999, Boyce 2000, Bader 2000, Murrow 2001, Maher *et al.* 2003, Larkin *et al.* 2004).

With restricted or reduced migration ability between patches, population pressures can increase (Wiens 1996), particularly during environmental constraints from forage crop failures, drought, or fire, all of which can naturally reduce major bear food sources and suitable habitat (Jonkel and Cowan 1970, Rogers 1987, Craighead *et al.* 1995, Powell *et al.* 1997). Because bear fecundity, reproduction, and recruitment rates are among the lowest of all terrestrial species (Craighead *et al.* 1995, Servheen *et al.* 1999), such pressures can cause detrimental impacts on naturally-fluctuating populations (Jonkel and Cowan 1970, Rogers 1976, 1987, Allendorf *et al.* 1991, Craighead *et al.* 1995, Craighead and Vyse 1996).

Like all Ursidae, sun bears require unrestricted access to forage on a constant basis to search for resources. In the tropics, the spatially- and temporally-patchy nature of primary sun bear foods (i.e. fruit, termites, and ants) necessitates constant movement and foraging to maintain proper health and survival. Limited movement among patches can reduce the sun bear's capacity to forage, maintain nutritional stability and health, mate, and recruit new individuals into the population. When such pressures occur during a natural population ebb or when demographic ratios for viable reproductive mates are low within or among patches, long-term sub-population and metapopulation persistences are reduced (Rogers 1987, 1976, Powell *et al.* 1997, Mattson 1998, Boyce 2000, Murrow 2001). Regardless of deleterious genetic consequences, the demographic effects from these events could lead to local sub-population extinctions (Craighead and Vyse 1996, Wiens 1997). Considering that sun bear populations are significantly reduced and isolated in fragmented patches (Servheen 1999a), the fate of local sun bear populations depends on understanding how landscape structure

affects individual movement patterns within and among patches (Wiens 1992, 1996, 1997, Augeri 1994, Noss *et al.* 1996, Craighead and Vyse 1996, Stacey *et al.* 1997, Ims and Yoccoz 1997, Boyce 2000, Bader 2000) and their access to critical resources and habitat (Rogers 1987, Craighead *et al.* 1995, Powell *et al.* 1997, Boyce and McDonald 1999, Mace *et al.* 1999).

CHAPTER 4

STUDY AREAS, FEASIBILITY STUDY



AND EXPERIMENTAL DESIGN



STUDY AREAS

4.1 Introduction

Three regions were compared (figure 4.1): (1) the Leuser Ecosystem (24,000 km²) in the provinces of Aceh and North Sumatra, Sumatra (2) Kayan Mentarang National Park (14,000 km²) in northwest East Kalimantan along the interior mountains bordering Sarawak and Sabah, Malaysia, and (3) the Bulungan Research Forest (4,226 km²), bordering the eastern edge of Kayan Mentarang in the lowlands of the Malinau and Seturan watersheds of northern East Kalimantan. All of these sites are considered some of the most diverse and biologically-rich regions in the world (IUCN/WWF 1994, MacKinnon *et al.* 1996, Momberg 1998, Whitten *et al.* 2000, Meijaard *et al.* 2005) and current and historical evidence indicate sun bear activity in each.

This study area configuration allowed comparison of 16 survey sites dispersed among 6 focal areas in 3 regional ecosystems on the 2 islands. These sites each harbour a diverse matrix of the most prevalent and unique habitat types in the region and are subjected to similar disturbances, such as logging, commercial timber and crop plantations, roads, local farms, fire, mining, village expansion, human traffic and other activities, wildlife hunting, and forest-product gathering, to mention a few. Comparisons between the study areas enabled analyses of sun bear ecology and habitat use in similar and distinct biogeographic situations in disturbed and undisturbed habitats across the bear's range in Indonesia.



Figure 4.1. Map of the Malay Archipelago and this study's primary focal areas: the Leuser Ecosystem, Kayan Mentarang National Park, and the Bulungan Research Forest.

Two staffed field stations in the Leuser Ecosystem and one each in the East Kalimantan sites were used as field bases. These sites were isolated from each other by extensive geophysical barriers and their respective situations provided opportunities to study disturbed and undisturbed sun bear populations and habitats in various biogeographic conditions within the same ecosystems and between regions with minimal interaction effects.

4.2 Sumatra

Sumatra supports broad altitudinal and ecotype gradients of vegetation types within the sun bear's range. The oldest known Sumatran forests were primaeval swamp forests that formed during the Carboniferous period about 300 million years ago (mya) (Whitten *et al.* 2000). Much of the island was altered by various volcanic, geologic, limestone forming, oceanic, and sedimentary episodes. These events created today's inland zonal, podsolised, and limestone soils that support primary sun bear habitat of lowland forests up to 1,200m asl, including heath forests. Today, similar swamp forest ecotypes exist where lowland oligotrophic and eutrophic soils support brackish water, freshwater, and peat swamp forests. Zonal soils also maintain lower montane forests between 1,200 – 2,100 m asl, upper montane forests between 2,100 – 3,000 m asl, and tropical sub-alpine forests above 3,000 m asl. Dipterocarpaceae trees, such as *Dryobalanops, Dipterocarpus, Parashorea*, and *Shorea* dominate much of the lowland forests (112 species, of which 11 are endemic) and form a continuous canopy where this habitat is protected (Whitten *et al.* 2000).

Although these forests are dominated by Dipterocarpaceae, lowland forests are also the richest and most biologically-diverse vegetation type on the island, where at least 80 different tree species greater than 15 cm dbh (diameter at breast height) have been recorded in 0.5 ha plots, supporting at least 245 different bird species (Whitten *et al.* 2000). In one valley, the Simpson index of diversity (*D*) for trees of 15 cm dbh or greater was 0.96 and in the adjacent hills it was 0.93 (McKinnon 1974). Data from the present study show the mean Shannon-Weiner index for trees ≥ 10 cm dbh was quite high (H = 5.1) in 0.2 ha plots in the eastern plain and slopes of Gunung Leuser National Park. Sumatran floral diversity tends to decline along an elevation gradient, where plant and tree species diversity and abundance are most extensive in the lowland valleys (50 – 80 tree species/0.5 ha), declining with increasing altitude to upper montane forests (18 tree species/0.5 ha) (FAO/MacKinnon 1982).

As observed in other bear species (*see* Jonkel and Cowan 1971, Rogers 1976, 1987, Powell *et al.* 1997, Craighead *et al.* 1995, Craighead WWI 2000), sun bear ranging patterns appear to be correlated with this floral elevation gradient due to the basic distribution and abundance of particular foods (Augeri 2003). For sun bears, distributions are generally

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linked to fruits, bee hives, and termites (Augeri 2002, 2003), although other food items are important in sun bear diets (Fredriksson 2001, Wong 2002). Gregarious fruiting occurs, which supplies high quantities of fruits and seeds in specific locations, but it is restricted to just a few families, particularly Dipterocarpaceae (Whitten *et al.* 2000). There is considerable variation within and between species, locations, months, and years in the vast majority of other Sumatran fruit, flower, and leaf productions (Whitten *et al.* 2000). Sun bears are seed dispersing-agents for a very diverse and broad array of fruits (McConkey and Galetti 1999, Augeri 2001, Frediksson 2001), but most of these trees and plants are pollinated by insects, which vary in abundance and geographic extent due to environmental and predatory variations. Consequently, fruit and insects are highly capricious in abundance and location. Although there is a diverse group of important fruits available to sun bears, including 100 recorded species of *Ficus* spp. (Leuser Management Unit 1999), the biogeographic availability of most primary bear foods are important influences on sun bear foraging and ranging patterns in both disturbed and undisturbed landscapes (Augeri 2003).

Sumatra's diverse flora supports one of the richest faunas in Indonesia, including the highest number of mammals (201 species, of which 23 are endemic) and second highest number of birds (580 species) (Whitten *et al.* 2000). It also sustains 22 species of Asian mammals that do not exist elsewhere in Indonesia, including the Asiatic golden cat (*Felis temmincki*), tapir (*Tapirus indicus*), lar gibbon (*Hylobates lar*), siamang (*Hylobates syndactylus*), and mountain goat (*Capricornis sumatraensis*). Several mammals, which are extinct in other regions of Indonesia and still range on Sumatra include the Sumatran rhinoceros (*Dicerorhinus sumatrensis*), elephant (*Elephas maximus*), tiger (*Panthera tigris sumatrae*), and dhole (*Cuon alpinus*). This diversity is primarily due to Sumatra's large land mass, geologic diversity supporting a wide-range of habitat types, and its past links with the Malay Peninsula of mainland Asia (Whitten *et al.* 2000).

As of the year 2000, less than 10% of Sumatra's natural vegetation types were protected (Whitten *et al.* 2000, WRI 2001). By 2000, between 2/3 - 4/5 of the sun bear's preferred habitat of lowland forests had been cleared for timber, agriculture, development, roads, and so forth (Whitten *et al.* 2000). Land-use conflicts and logging throughout the island are more extensive today (WRI 2004). Of the primary vegetation types remaining by 1996 that were known to be used by sun bears, only 5% of the original semi-evergreen lowland forests, 32% of evergreen lowland forests, a maximum of 4% of heath forests, 29% of ironwood forests, 8% of freshwater swamp, 58% of peat swamp, and 60% of montane forests remained (Whitten *et al.* 2000). By 2004, effective available habitat was more reduced (LMU unpubl. data).

4.2a The Leuser Ecosystem

Geography and Climate

The Leuser Ecosystem, which includes Gunung Leuser National Park (8,000 km²), is situated in the Sumatran provinces of Aceh and North Sumatra (figure 4.2) at about latitude 4.5° North and longitude 97° East. This ecosystem is considered one of the most diverse expanses of tropical rain forest in the world (Whitten *et al.* 2000). Comprising more than 24,000 km², the Leuser Ecosystem extends from the edge of the Indian Ocean to close to the Malacca Straits and includes an extremely rugged, topographically-diverse expanse of lowland wet, moist and dry forests, montane forests, moss and heath forests, mangroves, peat swamps, isolated sub-alpine meadows, two expansive mountain ranges over 3,000 m asl, two major volcanoes, three principal lakes, and nine extensive river systems that flow to both the east and west coasts of the island (Leuser Management Unit 1999, Whitten *et al.* 2000). The average annual rainfall is 2,544 mm and the mean daily temperature beneath lowland forest canopy rarely exceeds 26° C during the day or drops below 22° C at night (Leuser Management Unit 1999). The driest months are February and June/July and the wettest months are March/April and September/October/November (Whitten *et al.* 2000).



Figure 4.2. Map of northern Sumatra with the Leuser Ecosystem and Gunung Leuser National Park.

Flora and Fauna

The Leuser Ecosystem is characterised as a heterogeneous system of rain-forest communities (Whitten *et al.* 2000). Fruiting cycles are highly variable within and between species, months, seasons, years, and habitats. An estimated 45% of the 10,000 plant species recorded in the West Indo-Malayan region are found in the Leuser Ecosystem (Whitten *et al.* 2000). A broad altitudinal range of habitats and associated vegetation types are represented, where the most common vegetation type up to 500– 600 m asl is tropical lowland forest dominated by a continuous canopy of trees from the Dipterocarpaceae family, such as *Shorea, Dipterocarpus*, and *Dryobalanops*. A large diversity of important sun bear fruiting species are dispersed throughout these lowland forests (Leuser Management Unit 1999, Whitten *et al.* 2000).

Sun bear distributions in this study area are correlated with altitudinal gradients, where plant and tree species diversities and abundances are most extensive in the lowland valleys and decline with increasing elevation. In addition, logging, encroachment, and human use are influencing sun bear distributions (Whitten *et al.* 2000, Augeri 2002, 2003). Highly-valuable Dipterocarpaceae motivate increasingly extensive logging throughout the region, including within the national park (Robertson and van Schaik 2001, van Schaik and Robertson 2001, WRI 2004). Current data, as well as other reports (*see* Santiapillai and Santiapillai 1996, Servheen 1999a), indicate that habitat loss and disturbance are affecting sun bear distributions and densities throughout Sumatra.

The Leuser Ecosystem is one of the most biologically-rich and diverse regions in South-East Asia (Whitten et al. 2000). At least 95 species of reptiles and amphibians, 383 bird species, and 105 mammal species have been recorded (Leuser Management Unit 1999). Camera-trapping and sign data from this study show sun bear activity in most undisturbed habitat types in the region, including at elevations of at least 2,143 m asl. Mammals of particular importance to sun bear ecology are primates, which are significant competitors for key fruits, and include notable species such as orang-utans (Pongo pygmaeus), gibbons (Hylobates spp.), macaques (Macaca spp.), and langurs (Presbytis thomasi). Other mammals with perhaps current and evolutionary influence on sun bears are predators like Sumatran tigers (Panthera tigris) and clouded leopards (Neofelis nebulosa). Present evidence and literature conflict on the pervasiveness of the clouded leopard in the Leuser Ecosystem, but camera-trapping data from this study indicate moderate clouded leopard activity in the Leuser study sites, with the second highest capture rate among large felids behind Felis temminickii. Like tigers, leopards can notably influence sun bear ecology through antagonistic interactions and possibly predation on cubs and juveniles.

Other species of conservation concern that would benefit from sun bear habitat conservation include the Sumatran elephant (*Elephas maximus*), rhinoceros (*Dicerorhinus sumatrensis*), and rare plants like Rafflesia (*Rafflesia* spp.). According to the Leuser Management Unit (1999) new records of plants, fish, bats, and insects, including six new species of termites (considered a key food item of sun bears) (Payne *et al.* 1985, Servheen 1989, Fredriksson 1998, 2001, Augeri 2000), are continually recorded in the area.

People and Disturbances

At least seven ethnic groups live in and around the Leuser Ecosystem. Although these groups do not include indigenous peoples, they do practice traditional methods of wildlife hunting and collection of forest products, such as wild honey, petai beans, rotan, swiftlet nests, gaharu, and damar. They also produce handcrafts from resources such as pandanus leaves and cultivate extensively within the ecosystem, particularly irrigated rice and fruit. In addition, the nearby metropolis of Medan, which is Indonesia's third most populous city, generates an epicentre of immigration to, and human activity in and around, the ecosystem. Disturbances that were within and bordering the ecosystem duirng this study were: (1) timber harvesting, (2) industrial crop plantations (palm oil, rubber, and corn including experimentation of genetically-modified varieties), (3) local gardens and cash-crop cultivation, (4) village expansion and development, (5) roads, (6) trails with low, moderate and high use, (7) fire, (8) portable log milling in the forest, (9) river, jeep, and truck traffic, (10) hunting/gathering and other human activities, and (11) domestic animal grazing.

Research Facilities

At the beginning of this project, there were five staffed field stations available, each with access to disturbed and undisturbed control sites and significantly isolated from each other by extensive geophysical barriers. Unfortunately, political and military unrest in Aceh and North Sumatra forced the local government and the Leuser Management Unit to close most sites in Aceh to foreign visitors and researchers and only two posts were available by September 2001. Those sites were:

(1) Ketambe—located in Aceh at the confluence of two river systems in lowland forest with access to high elevation habitats up to 3,000 m asl. This site is known historically for its high diversity and densities of mammals. Logging and poaching within the park in this area have increased substantially over the past decade and have influenced the presence of many species, including bears, tigers, and orang-utans (van Schaik and Robertson 2001). Consequently, potential disturbance influences on bears, tigers, and other species were compared in multiple disturbed and undisturbed habitats and biogeographic conditions along one of the largest altitudinal gradients in South-East Asia.

Aras Napal-located in North Sumatra and separated from Ketambe by an (2)extensive mountain range and human-altered lowland valley. This site is also situated in lowland forest along a major river with access to undisturbed primary forest up to 3,000 m asl. Disturbed lowland sites, plantations, and human use exist at low and higher elevations. Historically, the rich and diverse lowland ecosystem in this area harboured the full suite of species typical of this ecosystem, but extensive logging and oil palm plantation development have transformed much of the region bordering the park, as well as inside the park, since the 1970s. By the time of this study, these areas had 15 - 25 years of secondary forest regeneration bordering primary forest, plantations, gardens, and so on, which provided a diverse matrix of habitat and disturbance types for comparison. Expeditions to remote sites for several month periods were conducted where and when necessary and were based from the Elephant Patrol Unit in Aras Napal and from the villages of Tankahan and Ketambe.

In September 1999, four biologists from the Leuser Management Unit and Indonesian Institute of Sciences were killed in Aceh. By December 2001, the local and national governments along with the Leuser Management Unit were obliged to close the Ketambe station to everyone other than essential Acehenese maintenance staff. Thus, only the Aras Napal site was available to this study beginning in January 2002. Problems continued and rebels from the Free Aceh Movement (GAM) recently took the Ketambe station staff as hostages, who were eventually released on US \$20,000 ransom.

4.3 Borneo

Borneo (figure 4.3) is one of the most biologically-diverse regions on the planet and is composed of virtually every tropical ecotype in South-East Asia, from coral reefs, mangrove and tidal forests, and peat swamps to vast lowland rain forests, extensive riparian systems, rich limestone habitats, montane and heath forests, and sub-alpine systems (Whitmore 1984, IUCN/WWF 1994, MacKinnon *et al.* 1996). Several reports suggest sun bears occur in all habitat types in lowland forest < 500 m asl (*see* Payne *et al.* 1985, Stirling 1993, Servheen 1999a). Data from this study show that sun bear activity in northern East Kalimantan is more limited to undisturbed primary forests and the bear's predominant occurrence appears to be in low- to mid-elevation undisturbed forest 400 - 750 m asl.



Figure 4.3. Map of Borneo and its major protected areas.

The lowland rain forests of Borneo expanded and contracted several times during the Pleistocene, but these forests have a stable history and have remained unchanged in character and composition (MacKinnon *et al.* 1996). Müller (1970) reported fossil pollen records from Sarawak that reveal the earliest occurrence of Dipterocarpaceae on Borneo is about 30 mya. This long history enabled an extensive evolution of plant diversity (Whitmore 1984),

including 2,000 orchids (MacKinnon *et al.* 1996). The flora of Borneo is derived from both Australasia and Asia (Wallace 1880, MacKinnon *et al.* 1996) and is richer than the entire African continent (MacKinnon *et al.* 1996). As the third largest island on the planet, Borneo supports 10,000 - 15,000 plant species, compared to 8,000 - 10,000 for Sumatra, 8,500 for the Malay Peninsula, 7,000 for the Philippines, and 9,000 for New Guinea (Jacobs 1988). MacKinnon *et al.* (1996) noted that at least two thirds of all described tree species on Borneo are found only in lowland forest, where as many as 240 different species can be found within one hectare in Kalimantan. There are at least 3,000 tree species on Borneo. At least 60% of the Dipterocarpaceae (267 species) on the island are endemic (MacKinnon *et al.* 1996), Borneo is considered one of the world's top distribution sources for this commercially-prized timber (WRI 2004).

For every 1,000 m rise in elevation on the island, the temperature decreases about 5° C, which is equivalent to a latitudinal shift of 10° away from the equator (MacKinnon *et al.* 1996). This shift, along with the changing character of mountain soils with increasing altitude, generates nutrient-poor and acidic soils. The results are decreasing plant growth rates along with declines in biomass and leaf-litter production with increasing elevation (MacKinnon *et al.* 1996). Decomposers occur at lower densities in Bornean montane forests (Collins *et al.* 1984) and, consequently, the rate of decay and leaf-litter mixing are greatly reduced at higher elevations. Thus, tropical mountain flora on the island of Borneo occur in successive and distinct vegetation zones with different species, different structure, and different appearance (MacKinnon *et al.* 1996).

There are three parallel and major shifts in forest structure and appearance with increasing altitude on Borneo. In general, the three-layered lowland forest is progressively replaced by a two-layered and, ultimately, one-layered forest (Robins 1968). MacKinnon *et al.* (1996) noted that, as elevation increases, there is an initial decrease in height and biomass, while giant emergents in the lowland forest begin to decline and become absent from lower montane forest. During this progression leaf size decreases and the number of epiphytes increases, particularly bryophytes and filmy ferns. The most notable changes are in forest structure and species composition, where montane forests are dominated by slender, less-productive trees of fewer families. Borneo's incredible floral diversity in primary forests supports a wide range of food resources for sun bears, enabling bears to range from sea level to 2,300 m+ (Augeri 2003, Meijaard *et al.* 2005). As on Sumatra, sun bear distribution and density appear to be correlated with the floral altitudinal gradient, where major fruiting plant and tree species diversity and abundance are most extensive in the lowland valleys and decline with increasing altitude.

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Some important plant and tree families generally ranging below and above 1,000 m are noted in table 4.1. The general implications of such restrictions exist in floristic structure, composition, and productivity, with consequent decreases in faunal diversity and sun bear range. For example, oak/chestnut forest produce a high caloric food source for several bear species (Jonkel and Cowan1970, Rogers 1976, Stirling 1993, Craighead *et al.* 1995, Powell *et al.* 1997, Servheen *et al.* 1999, Craighead WWI 2000). On Borneo this important bear food is generally limited to 1,500 m asl (MacKinnon *et al.* 1996), which marks the average upper elevation range of sun bears (Payne *et al.* 1985, Stirling 1993, Augeri 2003). Oak/chestnut, however, is not the only resource influencing sun bear altitudinal range. The sun bear diet is diverse (Stirling 1993, Fredriksson 2001, Wong 2002, Augeri 2002, 2003) and extensive enough to support bears as high as 2,300 m asl on Gunung Kinabalu in Sabah (Payne *et al.* 1985) and > 1,500 m asl in Kayan Mentarang National Park (Augeri 2003). Both of the study areas on Borneo encompass a significant portion of sun bear habitats, from sea level to > 2,574 m asl.

generally limited in ranges below or above 1,	000 m asl (from MacKinnon et al. 1996).

Table 4.1. Some important plant families and genera occurring on Borneo that are

Major Plants ranging < 1,000m asl	Major Plant ranging > 1,000m asl	
Families Anacardiaceae Burseraceae Capparidaceae Combretaceae Connaraceae Dilleniaceae Dipterocarpaceae Flacourtiaceae Murietiaceae	Major Plant <u>Genera</u> Cardamine Drimys Galium Gaultheria Gentiana Gunnera Haloragis Netera Rammculus	Families Aceraceae Araucariaceae Clethraceae Ericaceae Fagaceae Lauraceae Myrtaceae Podocarpaceae Symplocaceae
Nyfisicaceae	Viola	Theaceae

4.3a Kayan Mentarang and Bulungan Ecosystems

Geography and Climate

Kayan Mentarang National Park (14,000 km²) is located in the northwest region of the Indonesian province East Kalimantan, Borneo along the borders of the Malaysian States of Sarawak and Sabah. The Park is situated at about latitude 3° North and longitude 116° East, (figure 4.4). The Bulungan Research Forest (BRF) borders Kayan Mentarang National Park's east boundary and encompasses 4,226 km² at about 3 degrees north of the equator at 2°45' to 3°21' North and 115°48' to 116°34' East (figure 4.4). The BRF is in the Malinau watershed of East Kalimantan's northern lowland forests and is part of the greater Bulungan Ecosystem, which is the centre of the largest area of semi-continuous rainforests remaining in tropical Asia (Meijaard et al. 2005). Although these forests are becoming more fragmented by roads, village expansion and large commercial oil palm plantations, the Bulungan Ecosystem comprises an area of more than 50,000 km² (including Kayan Mentarang National Park) encompassing parts of Central and East Kalimantan, Sarawak and Sabah (Meijaard et al. 2005). The combination of the Kayan Mentarang and Bulungan regions constitutes an unbroken altitudinal and habitat gradient from the interior mountains to the eastern lowlands. Thus, bear and habitat surveys were focussed on most representative habitat, vegetation, and ecosystem types in East Kalimantan.



Figure 4.4. Map of Borneo with Kayan Mentarang National Park and the Bulungan Research Forest.

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Rainfall patterns are determined by two main monsoon seasons in this region, a south-east or "dry" monsoon (May-October) and a northwest or "wet" monsoon (November-April) (MacKinnon *et al.* 1996). The elevation gradient of the study area ranges from 40–900 m asl in the BRF and 320 - 2,574 m asl in Kayan Mentarang. The central mountains of the Kayan Mentarang and Bulungan regions may receive between 2,000 - 4,000 mm of rain/year (MacKinnon *et al.* 1996). As the north-west monsoon passes from the west through this central mountain range, it becomes relatively weak once it reaches the east coast, where rainfall is often less than 200 mm/month (MacKinnon *et al.* 1996). Four major river systems and their tributaries extend from the interior mountains to the coast: the Kayan/Bahau, Malinau, Mentarang/Sesayap, and the Sembakung. Temperatures in lowland forests range between 25^0 C and 35^0 C +. Upper elevations range between 15^0 C and 20^0 C (MacKinnon *et al.* 1996).

Fauna and Flora

According to the WWF (S. Wulffraat pers. comm.), which is the main body assisting the Indonesian government with implementing research, monitoring, and conservation programmes in Kayan Mentarang National Park, conservation biology research has only just begun over the past 10 years. As of 1996, topographical data, reliable maps, and even basic species lists were lacking for much of the interior of Kalimantan (MacKinnon *et al.* 1996) and by 2005 only the most basic information was available. Nevertheless, it is recognised that this region embodies some of the highest species diversity and endemism in the world (IUCN/WWF 1994, MacKinnon *et al.* 1996, Momberg *et al.* 1998). Kalimantan's very high diversity is associated with soils over geologically-young rocks (MacKinnon *et al.* 1996), which creates heterogeneous forest structure and vegetation types that provide a diverse array of niches for both plants and animals (Dransfield 1992).

This remote study region is characterised by a rugged topographically-diverse matrix of habitat types (MacKinnon *et al.* 1996). The steep, hilly terrain is covered by tropical forest vegetation typical of central Borneo, but there is a high diversity and abundance of palm species that are used by both indigenous peoples and animals, including by sun bears for food when forest fruits are rare (Puri 1997). Nearly half of Kayan Mentarang National Park lies below 1,000 m asl and contains areas of species-rich Dipterocarpaceae forest and oak-laurel mountain forests with a high proportion of endemic species (Puri 1997). The western region of the study area comprises interior forested hills and mountains with limestone areas and outcrops that are recognised as centres of global plant diversity by the IUCN and WWF (1994). Mature montane forests are dominated by

families of Aceraceae, Araucariaceae, Clethraceae, Lauraceae, Myrtaceae, Podocarpaceae, and Theaceae (MacKinnon *et al.* 1996). Lowland forests in the park and eastward in the BRF are dominated by mature climax Dipterocarpaceae spp. with high canopy, clear stratification, and tall leguminous and dipterocarp emergents (MacKinnon *et al.* 1996). These lowlands are fed by nutrient-rich river corridors that support high densities of wildlife (Momberg *et al.* 1998). The study area extends into less species-rich heath forests on impoverished white sand soils, to fresh- and brackish-water swamp forests, and finally to the lowland plain extending to the coast.

Sun bear activity has been reported across the region (*see* Meijaard 1997, Momberg *et al.* 1998, Augeri 2000, Meijaard *et al.* 2005) and data from this study indicate that sun bears are most active in undisturbed primary forest between 400 – 750 m asl. The region is home to populations of many endangered and threatened species that would benefit from sun bear conservation and reserve plans. Some of these species include clouded leopard (*Neofelis nebulosa*), elephant (*Elephas maximus*), orang-utan (*Pongo pygmaeus*), flatheaded cat (*Felis plancipes*), marbled cat (*Felis marmorata*), banteng (*Bos javanicus*), Bornean gibbon (*Hylobates muelleri*), proboscis monkey (*Nasalis larvatus*), long-tailed macaque (*Macaca fascicularis*), Bornean peacock pheasant (*Polyplecton schleiermacheri*), wrinkled hornbill (*Rhyticeros corrugatus*), possibly Sumatran rhinoceros (*Dicerorhinus sumatrensis*), and even crocodile (*Crocodylus porosus*) in the mangrove and tidal forests and wetland systems further inland.

People and Disturbances

Human population densities are not known for the entire study area, but by 1997 Puri (1997) suggested there were perhaps as many as 10,000 indigenous Lun Dayeh, Kenyah, Kayan, and Penan people within and bordering Kayan Mentarang National Park. Immigrants from Java and other islands also inhabit the region, primarily along the river systems. MacKinnon *et al.* (1996) noted there was a 4.42% increase in population in East Kalimantan from 1980 to 1986, but it is probably much higher today. The indigenous population in the Malinau watershed consists of Punan, Kenyah, Merap and other ethinic peoples (Puri 2001), but the number of immigrants has changed rapidly due the needs of logging concessions, estate plantations, coal mines, and road-builders for both skilled and unskilled labour. Consequently, the outside work-force has increased its influence, particularly a small but growing population of Javanese and Madurese transmigrants (Meijaard *et al.* 2005). While the majority of increase is restricted to major cities and towns, interior villages are also expanding (Augeri 1991, 2001, MacKinnon *et al.* 1996, T. Jessup pers. comm.). Nevertheless, human densities in the region are low relative to other areas.

Throughout the remote areas, the main sources of income and livelihood are swidden farming, hunting, river transport and other services, and collection of valuable forest products, e.g. bird nests and aromatic woods or "gaharu" (a derivative from *Aquilaria* spp.). In general, wild forest products provide most communities with subsistence needs, particularly from wild animals. Indeed, the WWF Lalut Birai research station derives the majority of its protein from within the national park – all of which was hunted and sold by local villagers as well as some staff. The primary protein sources at Lalut Birai still consumed at the time of this writing were bearded pig (*Sus barbatus*), muntjac (*Muntiacus spp.*), and sambar deer (*Cervus unicolor*), but many other species were consumed on an opportunistic or semi-regular basis at the station, including macaque (*Macaca spp.*), Argus pheasant (*Argusianus argus*), langur (*Presbytis spp.*), pangolin (*Manis javanica*), mouse deer (*Tragulus spp.*), and even python (*Python reticulatus*), to mention a few (D.M. Augeri unpubl. data).

It is important to note that there is a significant cultural connection in this region to many forest products, including those used as ornaments, such as sun bear and clouded leopard teeth, skins, and claws, hornbill feathers, and so forth (D.M. Augeri, unpubl. data, Meijaard *et al.* 2005). Hunting methods are often with shotguns, but ammunition is expensive. Thus, the most popular method for hunting larger animals remains the use of dogs to chase and corner target species, which are then killed with spears or guns (pers. obs.). Poisoned darts from blowpipes also remains popular for more sensitive species, because guns tend to scare animal groups (Puri 1997, Meijaard *et al.* 2005, pers. obs.).

There have been long-standing traditional prohibitions on eating many wildlife species and many older people avoid monkey and snake meat, while women will not eat bear (D. Sheil unpubl. data as cited in Meijaard *et al.* 2005). Nevertheless, the Christian church has demystified many of these taboos over the past few decades and both meat trading and trade of wild animals are becoming increasingly-important sources of income (pers. obs.). Many species are trapped, traded, and sold by local villagers, outsiders, profiteers from down river or the coast areas, and research station staff. Many of the target species include a variety of protected species, such as sun bears, primates, and blue-crowned hanging parrots (*Loriculus galgulus*) for trade, and many restaurants serve a variety of protected and non-protected species (D.M. Augeri unpubl. data). A trade in live animals for halal killing (for Muslim consumption) is also developing in Malinau and in outlying areas (Meijard *et al.* 2005, pers. obs.). Improved transportation by roads, rivers and light plane help supply

(illegally in some cases) the increasing demand for meat and pets from the interior to major towns and cities. Bennett and Robinson (2000) and Meijaard (2003) report that hunting has become unsustainable in Kayan Mentarang National Park and portions of Sarawak.

Many large road building projects are in progress and include road corridors connecting Malinau with the eastern villages of Kayan Mentarang National Park and the upper Baram area in Sarawak. The ecological impacts of these main roads are notable, but the predictable side roads, tracks, trails, outposts, and new villages developed off the main roads significantly fragment the landscape (Augeri 2002, Meijaard *et al.* 2005). This is particularly the case given the accompanying rights provided to road development companies to extract timber from 1 km strips of forest on either side of the roads.

Other disturbances and competing land uses during this study included: (1) oil-palm plantations; (2) industrial logging and timber plantations; (3) coal and gem mining; (4) oil/gas exploration; (5) fishing, hunting and trapping; (6) collection of forest products (fruit trees, sago palms, rattan, and aromatic woods), (7) local cash-crop cultivation and farming (irrigated rice fields, mixed crop swiddens, etc.), (8) transmigration projects, (9) fire, (10) village expansion, (11) truck, car, boat, and foot traffic, (12) and trails. Secondary forests of varying ages are found along the banks of major rivers, but generally do not extend beyond the first ridge, while mature forest is found close to major rivers, as well as throughout the interior (Puri 1997). Wilson and Wilson (1975) noted that Bornean species particularly disturbed by logging include the sun bear.

Research Facilities

Kavan Mentarang National Park Data were collected in Kayan Mentarang National Park from the main staffed field station, Lalut Birai, operated by the WWF-Indonesia Kayan Mentarang Project. The station is situated near the mouth of the Nnggeng River, where it joins with the headwaters of the northern tributaries of the Lurah, Jalungkereng, and Nnggeng Stee rivers, eventually flowing into the upper Bahau River. The Nnggeng river valley serves as an important corridor leading from the edge of the park at the Bahau River into the mountainous interior, ranging in elevation from about 300 m asl to 2,574 m asl. This remote region is a critical core zone of about 10,000 ha of undisturbed habitats that support many endangered species as well as traditional hunting for local Dayak communities (Puri 1997, pers. obs.). Hunting, gathering, and research activities occur inside the Park in the Lalut Birai area and further interior, while rotation swidden agriculture, hunting, logging, and other activities are conducted on the Park's eastern boundary and along portions of the

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west bank of the Bahau River. Consequently, protected primary forests, hunted primary forests, secondary forests aged 1 - 25+ years, and newly-cleared areas were surveyed within the same ecosystem. Expeditions to remote sites for several month periods were conducted where and when necessary and were based from Lalut Birai and the village of Long Alango, ca. 10 km north along the Bahau River.

Bulungan Research Forest Field work in the Bulungan Research Forest was based from the Seturan Field Research Station, operated by the Centre For International Forestry Research (CIFOR). The station is situated along the Seturan River, which is a major tributary of the Malinau river and is about 20 km south of the village of Long Loreh and about 70 km south of the town of Malinau. The area is deeply eroded and dominated by rich primary lowland forest ranging in elevation from 40 - 900 m asl. Soils are diverse, but very poor in the nutrients that support plant growth (Basuki and Sheil 2005). According to Meijaard *et al.* (2005), most of the suitable areas for rice in the area are either under cultivation or lie fallow, but nutrient content is low and flood risks are generally high.

The BRF is also the site of a 48,000 ha state-owned logging concession run by PT Inhutani II, where conventional logging (CNV) and Reduced Impact Logging (RIL) are practised. Subsistence hunting is still practiced in the area, as well as hunting for meat to sell to logging concession workers, local villages, and the town of Malinau. Gathering of non-timber forest products is also a regular activity along with collection of bird nests, animals, and plants. Thus, undisturbed primary forest, disturbed primary forest, hunted forest, secondary forests ranging in age from $1 - 10^+$ years, and newly-cleared areas were surveyed within the same ecosystem. Expeditions to remote sites for several month periods were conducted where and when necessary and were based from the Seturan field station and village of Long Loreh about 20 km north of the field station.

4.4 Feasibility Study

Project feasibility studies were conducted in October and November 1998 and preliminary research occurred during February – March 2000 (Augeri 2000). This initial field work involved testing methods and habitat bias, training local biologists, conducting preliminary surveys, securing permits, and meeting with Indonesian collaborators and counter-parts. Sign surveys were conducted in various biogeographic conditions in undisturbed and disturbed habitats in Aras Napal of the Leuser Ecosystem, North Sumatra and in Kayan Mentarang National Park and border areas in East Kalimantan.

By the mid 1990s no sun bears had been successfully trapped for research purposes and it was clear that indirect methods, such as camera-trapping, sign surveys, and genetic sampling, could be useful for examining sun bear ecology and landscape use. Sun bears leave more conspicuous and persistent signs than other bears (Stirling 1993, Augeri 1999) and other tropical forest species, including civets, marten, ungulates, and primates (Payne *et al.* 1985, Augeri 2000), enabling more indirect methods. This supposition was first supported by six weeks of feasibility work in 1998, during which opportunistic observations were conducted on the behaviour and signs of three free-ranging habituated sun bears (one adult female, one juvenile female, and one male cub), as well as signs left by wild sun bears around trapping sites, trails, and throughout the Sungai Wain Protection Forest in East Kalimantan. My feasibility studies at Sungai Wain were by courtesy of the Wanariset in Samboja (Balikpapan), East Kalimantan, the Indonesian Forestry Department, and the Camp Djamaludin coordinator, Gabriella Frediksson.

I observed the habituated bears and their distinct signs over about 23 days, including termite and ant excavations, tracks, hairs, scats, torn logs, and claw-marked trees climbed for fruit, bee hives, and insects. Behavioural observations were intermittent and opportunistic, amounting to ca. 50 hours during this period, and were most often restricted to the camp area and edge forest and during sporadic forrays further in the forest. These observations were compared with my previous studies in Kalimantan in 1990 – 1991 (Augeri 1991) and with my former studies of *U. arctos, U. americanus,* and *U. maritimus* in North America. Examples of sun bear behaviour and signs I examined and compared during this period were:

- (2) the sizes, depths and angles of claw marks and tracks
- (3) basic movement behaviour and patterns in various habitats
- (4) general characteristics of tracks during slow walking vs. faster movements
- (5) general foraging behaviour, eating styles, and associated sign left behind
- (6) food types selected/discarded and general behaviour patterns in the forest
- (7) differences between bear and other species signs

⁽¹⁾ climbing and descending trees, tearing logs, digging for termites, etc.

- (8) bear interactions with other species
- (9) all other observable signs as well as tree nests and log dens, etc.

I also provided assistance to G. Fredriksson with trapping wild sun bears, through which I was able to age bear and other animal signs to within 24 hours of the animal's visit to the trap sites where there had not been bear signs during previous checks. Signs by bearded pigs, deer, civets, marten, and other species were also studied and were verified by direct sightings, back-tracking, and other distinct signs like spoor and scat (Augeri 1999).

I was also able to participate in processing the habituated juvenile female sun bear with D. Garshelis and G. Fredriksson. While it was sedated I examined the bear's morphology, hair, paws, claws, and other physical characteristics more closely. In another instance, locals reported an adult sun bear fleeing a hollow log and D. Garshelis and I were invited to help G. Fredriksson examine the signs and hairs left behind at that site. Evidence indicated the log was possibly being used as a den (G. Fredriksson pers. comm., D. Augeri pers. obs.). In 2000, I was asked to help process and radio-collar one tranquilised wild adult female sun bear that was trapped by G. Fredriksson and her team at Sungai Wain. In addition to examining the signs left by this bear at the trap site, I was also able to examine closely the physical features and morphology of this bear while it was under sedation. These and other events were key portions of this feasibility work through which I observed and compared definitive sun bear signs, behaviour, and ecology of known individuals.

Habitat bias was examined at the different sights in 1998 by marking different tree species in the form of claw marks with a machete and then examining the aging process of these and known bear signs every few days during this study period. Because habitat traits, such as tree species, bark type and thickness, exposure, rain, temperature, and other environmental conditions can bias sign age estimates, more extensive tests of aging were conducted in 2000. Sign age and habitat bias are important aspects of this research and these were tested in both East Kalimantan and North Sumatra via simulated tree markings with machete in the form of bear claw marks on various tree species, as well as simulated termite diggings and tracks in different habitat types. In particular, 10 representative samples of known sun bear focal tree species of different ages studied in 1998 were selected randomly at each site. In East Kalimantan, for example, these were represented in the families Euphorbiaceae, Fagaceae, Lauraceae, Moraceae, Myrtaceae, and Sapindaceae. Bear claw marks of various sizes, depths, and weights intended to represent different bear age classes were simulated using a machete. Aging of all test marks was then studied on a 3-5 day basis over 6 weeks. Signs of aging included cambium and inner wood deterioration, colour changing, bark growth, peeling, and so on. Other sign tests included simulated termite

colony diggings in different substrates, slopes, and biogeographic conditions (e.g. exposed, full-canopy cover, etc.), back-tracking of animals immediately after identification, testing simulated bear prints in various substrates using bare human foot prints (which are very similar to bear prints), and scat deterioration from domestic dogs. Results from all aspects of these field trials were positive and the field methods proved viable and realistic.

In February and March 2000, a total of 14,000 m of Fixed-width transect censuses were conducted as part of more extensive field trials. Eight 1,000 x 10 m transects were conducted in the Leuser Ecosystem and six 1,000 x 10 m transects were conducted in Kayan Mentarang National Park and border areas. These surveys included six different habitat types (table 4.2): (1) undisturbed primary forest; (2) 20+ year-old post-cut secondary forest; (3) 1 - 5 year-old post-clear-cut growth; (4) secondary forest edge habitat bordering oil palm and citrus plantations; (5) a citrus plantation bordering secondary forest; and (6) an oil palm plantation bordering 5 - 20 year-old secondary forest.

Each transect was surveyed systematically by myself and two trained local field assistants spaced 2.5 m from me as I walked along and censused a 2.5 m strip of the transect centre line. An average of 12 observer hours/1 km transect in the Leuser Ecosystem and 15 observer hours/1 km transect in Kayan Mentarang were spent on the surveys. Field assistants were local Indonesian biologists with Indonesian NGOs, each with multiple years of ecological experience in the specific survey sites. These assistants were further trained by me in wildlife ecology, animal signs, natural history and tracking, forest ecology, tree stand surveying methods, Distance (line-transect) and Fixed-with surveying techniques, mapping and compass skills, and hand-held GPS surveying. Observer reliability was tested by training these assistants with simulated signs, for which the age and source of the signs were only known to me. Assistants were also trained in recording tree height, canopy and ground covers, slope, aspect, and elevation in different habitat types. This training was highly beneficial, resulting in high observer reliability. Accuracy and consistency were measured by testing the assistants' abilities in sign age estimation, canopy cover, tree height, and slope calculations, and all other field methods. Within one week, mean assistant accuracy was about 76% and method consistency was provided for each transect and habitat type.

All transects were randomly located off trails, measured with a hip-chain and GPS, and conducted in straight lines according to random compass bearings. In only a couple of cases, logistical considerations (i.e. conducting edge surveys parallel to plantations) were necessary, in addition to ecological parameters (e.g. slope contours, water barriers), for determining transect direction. Both compass and GPS coordinates were mapped for all transects and each sign type was photographed (Augeri 2000).
4.4a 2000 Preliminary Results

Augeri (2000) reported frequency analyses (table 4.2), one-way ANOVA, and Chisquare tests on sun bear use of all six different habitat types based on bear sign evidence. Sun bear signs were very distinct and surveys resulted in high confidence. Verified evidence on these surveys included: claw-marked trees; torn logs; spoor; excavated termite colonies, bee hives and ant colonies; day-bed and denning sites; scat; and food debris. The majority (87%) of claw-marked trees were greater than 20 cm dbh. The majority (62%) of signs were < 1 year old. Although the total number of transects was relatively small (n=14) and many more surveys were required, statistical results (F = 10.64, P = 0.0022; $X^2 = 12.76$, P = 0.0052) and frequency results indicated a noticeable difference in bear sign frequencies among the six different habitat types (Augeri 2000).

These preliminary surveys indicated that regardless of the region or biogeographic characteristics (e.g. Sumatra or Borneo), a noticeably higher frequency of bear signs existed in different habitat types, as well as in primary and older secondary forest compared to younger post-cut secondary forest, disturbed areas, and edge habitat. Given that one of the primary objectives for this project was to compare differential habitat use by bears, particularly relative to different habitat and disturbance types, results indicated that these methods were viable and could generate substantive data on potential biogeographic and disturbance effects on relative habitat use by sun bears. To answer the questions for this study with appropriate sample sizes and statistical rigour, integrating sign surveys, habitat and forage productivity assessments, tree stand surveys, and capture-recapture systems by camera trapping and genetic sampling were clearly effective field methods (Augeri 2000).

Habitat Type	Mean Number of Sign Events	Total Transects	S
Primary Forest (undisturbed)	23.5	4	7.94
Secondary Forest (>20 yr)	6.7	3	0.58
1-5 yr Post-cut Growth	2.0	3	1.00
Edge of Secondary Forest	0.5	2	0.71
Oil Palm Plantation	2.0	1	
Citrus Plantation	0.0	1	

Table 4.2. Frequency analysis of preliminary survey results for six habitat types and associated standard deviations (s).

4.5a Sampling Design

Differences among multiple variables and their interactions were tested by the statistical scheme described below. Specific method and test details are discussed in Chapters 5 and 6. Because greater coverage of the sampling universe produces less variability among surveys and more accurate results and generalisations, a representative sample of 50 habitat types and conditions, 44 disturbance types, and 60 human activity types were surveyed in 16 study sites across 6 focal areas of broad geographic extent, in 3 regional ecosystems on two distinct islands (Sumatra and Borneo) separated by > 1,000 km. Primary undisturbed forests (with nested habitats, such as swamps, montane forests, heath forests, and so forth) were used as the control treatment for all analyses. Surveys were conducted across multiple seasons and years in October – November 1998, February – March 2000, and continuously for a 32 month period during September 2001 – May 2004. Surveys were conducted simultaneously by multiple teams on Sumatra and Borneo.

A stratified-random sampling design was used as the main template for data collection. To ensure that a sufficient sample of ecological conditions and habitats were represented, focal areas were stratified *a priori* based on known ecological and topographic features, habitat type, elevation, proximity to and types of disturbances, including areas with and without hunting, government permits, accessibility, and location of research facilities. Maps for some sites were not available and, thus, stratifying sites based on aerial extent was not possible. Depending on the focal area and map availability, a 1 or 2 km² grid system was overlaid on topographic maps and, where available, habitat classification maps derived from existing GIS data layers, the latest TM 10 m panchrome data from Landsat 7, or aerial photographs. A stratified random sample of survey sites were then selected within each focal area, such that $48 - 64 \text{ km}^2$ sites were randomly delineated to encompass a representative sample of habitat and disturbance types with varying topographic and biogeographic features within each survey block. Because randomisation procedures provide robust statistical power (Ott 1988, Ott and Longnecker 2001), transects or camera-trap sites were randomly placed in each grid cell. Each transect and grid cell was numbered using a random numbers table. Other studies (Bourn et al. 1999) suggest to then select a 5% random sample, but such samples are drawn from the entire sampling universe (i.e. all sites combined). In this case, a 50% sample per site was more appropriate for this design to satisfy random sample sizes of > 20 per site (Ott 1988). For camera-trapping, two camera-trap sites/4 km² were randomly positioned in the field in each 48 km² (Kalimantan) or 64 km² (Sumatra) survey site.

4.5b Sign Surveys

Randomised sampling periods decrease selection bias and, thus, surveys were conducted during random periods within each season to coincide with seasonal changes in bear food selection and behaviour (Garshelis 1991). Whenever possible, an equal number of surveys were conducted across sites. Study design followed randomisation theory and minimum sample sizes of $n \ge 25$ transects were achieved in most areas. In some cases where habitat or geographic area was limited, it was not possible to conduct 25 or more transects in one site, but more surveys were conducted in the same habitat types in other sites to increase sample sizes to appropriate levels for those types.

An average systematic sun bear sign census conducted by a three-person team along a 1,000 x 10 m transect required 7 – 10 hours, excluding foot travel to and from the survey site. Tree stand and fruit productivity assessments added an average of 1.5 - 2 hours/transect. Due to the logistics of accessing different areas and extremely rugged and difficult conditions at some sites, 3 – 5 transects/week were successfully completed for a total of 321 km of transects from 3 September 2001 to 8 July 2003. Specific methods and results are described in Chapter 5.

Kendall *et al.* (1992) recommended that 500 - 1,000 survey units (i.e. subdivided segments along a transect) are necessary to achieve good statistical power, which is defined as the probability of correctly rejecting a null hypothesis that is false (Steidl *et al.* 1997). In this study, 32,100 survey units of 10 m, 3,210 survey units of 100 m, 1,605 survey units of 200 m, and 642 survey units of 500 m were completed. Various analyses were conducted at each level (*see* Chapter 5).

4.5c Camera Trapping

Camera-trapping sample sizes were achieved by (1) generating sufficient coverage of the survey sites based on the ecology of sun bears and Sumatran tigers, (2) logistical considerations of access and camera-checks by foot within 5 – 7 day periods, and (3) funding and the total number of cameras and assistants that could be employed. Specific methods are discussed in Chapter 6. Coverage was based on average sun bear next of kin (*Ursus americanus*) female home ranges ($\approx 12 - 20 \text{ km}^2$), telemetry data of sun bear home ranges from Wong (2002) and G. Fredriksson (pers. comm.) of about 4 – 16 km², and the minimum known female tiger home range of about 15 km² (Karanth and Nichols 2000). To maintain consistency with sign surveys, 48 – 64 km² camera-trapping grids were overlaid in the same sites as sign surveys, which provided ample coverage of several sun bear home ranges per survey. A strategy of maximising trap density was used to enhance trapping success, such

that 2 trap sites were randomly positioned in every 4 km² grid, producing 32 trap sites/survey in Sumatra and 24 trap sites/survey in East Kalimantan. Surveys were conducted for 8 - 10 week periods according to specific protocols (Chapter 6) (Karanth and Nichols 1998, 2000). The same stratified-random sampling design was used as with sign surveys and were conducted in 10 stratified-random sites using at total of 280 camera-trap stations during November 2001 – May 2004.

4.5d Sample Sizes

In general, as sample size increases statistical test power increases, thereby reducing error variance and increasing test sensitivity for detecting treatment effects or differences in the focal populations (Fowler *et al.* 1998, Ott and Longnecker 2001). Larger sample size will also decrease Type I and II inference errors by decreasing error variance and increasing significance levels, thus reducing the likelihood of rejecting the null hypothesis when it is true (Type I) or accepting the null hypothesis when it is actually false (Type II). Decreasing such inference increases test power and sensitivity (Fowler *et al.* 1998, Ott and Longnecker 2001).

Given the variability in natural systems, statistical power is important for ecological research. Essentially, statistical power is not only a function of sample size, but also of α (the acceptable rate of Type I error) and effect size. Effect is defined as the degree to which a phenomenon of interest is present or changed by a particular treatment and is the minimum response that is considered biologically significant (Steidl *et al.* 1997). Effect size is simply *effect* scaled by standard deviation (Steidl *et al.* 1997). Increasing sample size, α , or effect size invariably increases power (Cohen 1988). Thus, to ensure robust statistical power and enable geographically-extensive monitoring, the following sampling scheme was used:

- (1) A randomised sampling design as described above and in Chapters 5 and 6.
- (2) The number of censuses were maximised, where 12 months/year for 22.5 months were spent conducting sign surveys and about 10 months/year over 32 months were spent for camera-trapping. At an average of 3 5 sign surveys/week, this generated 175 censuses (1,000 x 10 m each) for the Leuser Ecosystem and 146 censuses (1,000 x 10m each) for the East Kalimantan focal areas for use in these analyses. Camera-trapping produced 6 surveys in Sumatra and 4 surveys in East Kalimantan
- (3) Each transect was subdivided into 10 m and 100 m survey units per 1,000 m transect. This produced a minimum sample size of 1,750 survey units (100 m ea.) for the Leuser Ecosystem sites and 1,460 survey units (100 m ea.) for the East Kalimantan sites, thereby achieving good statistical power *via* this method.

- (4) Replication was achieved *via* random parallel and perpendicular transects and random camera-trapping sites within the same habitat blocks within seasons and years (*see* Chapters 5 and 6).
- (5) Redundancy was achieved by using multiple methods (i.e. Distance sampling, Fixed-width sampling, camera-trapping, and genetic sampling) in the same and different sites and periods, simultaneously by multiple teams (Chapters 5 and 6).
- (6) Statistical tests were conducted under a two-stage nested experimental design (described below), which tested grouped means of, for example, bear sign frequencies in similar habitat or disturbance types.
- (7) Statistical tests were conducted between years and data were pooled from multiple years to examine year-to-year fluctuations in habitat use and detectability.
- (8) Statistical tests were conducted within years and annual data were pooled to examine seasonal variation in sign and photo densities, bear behaviour, etc. (Garshelis 1991, Kendall *et al.* 1992, Steidl *et al.* 1997, Powell *et al.* 1997).

4.5e Two-Stage Nested Experimental Test Design

Due to potential violations of independence among observations as well as among potentially linked variables (i.e. elevation and fruiting) at the 10 m and 100 m levels, a twostaged nested experimental design was used to group data according to their associated transect or camera-trap site among habitat types, common elevations, disturbed and undisturbed sites, survey sites, focal areas, regions, and so forth (Augeri 1995). Grouped means were then tested among treatments (Augeri 1995). Grouping increased test power by decreasing (a) violations of independence, (b) assumptions of inter-dependence among variables, (c) variance and systematic error within and between surveys, and (d) variance and bias between surveys, treatments, and observers. This design enabled higher and more robust test power so that treatment effects could be tested on grouped means according to a two-stage nested experimental test design (figure 4.5).

	Selectively Logged		Undisturbed			
	Transect 001	Transect 002	Transect 003	Transect 001	Transect 002	Transect 003
Primary Lowland Forest					S	
Swamp Forest		S				
Montane Oak- Laural Forest			S			

Figure 4.5. An example of a Two-Stage Nested experimental design, where bear sign 'S' is grouped according to its common transect (columns) within each habitat (rows) within each treatment block (disturbed vs. undisturbed).

Under a two-staged nested experimental design, each variable (e.g. the presence of bear sign at 1 m resolution) was nested according to its common test group (e.g. transect at 1,000 m resolution) within its treatment (e.g. primary forest or disturbed habitat type). This design generated "grouped" test sampling units for every variable and the procedure was repeated for each habitat and disturbance type. All test calculations for that variable were then averaged together across their test group in SAS (SAS Institute 2002). The resulting mean generated one "grouped" or "pooled" sampling unit for that variable per transect in a particular habitat type in disturbed or undisturbed areas.

The above procedure was repeated for all test variables. Independent variables like canopy cover or fruit abundance were also tested in this manner to examine (1) differences among treatments, biogeographic conditions, and so on for these parameters as dependent variables, (2) possible correlations with, say, topographic or disturbance effects on these variables, and (3) statistically-sound grouped means for these variables to test their effects as independent parameters on bear sign frequency. All grouped sampling units were then tested for differences within and among treatments. This nested and grouped experimental design increased test power and robustness and, thus, treatment effects could be tested with minimal statistical bias for most variables and treatments. Consequently, tests at micro-site, patch, and landscape scales were possible (Augeri 1995).

4.6 General Study Assumptions and Limitations

Assumptions and limitations for particular methods are summarised in their respective sections. The following limitations apply to this study as a whole. In general, the field research portion of this project was logistically and physically difficult, which presented some statistical challenges. Indeed, these are some of the primary reasons why data on sun bears and other elusive tropical species like tigers and leopards have been lacking. Logistical challenges that influenced statistical analyses included:

- (1) Elusive and shy sun bear behaviour, which limited sightability and capture probabilities.
- (2) Limited sign persistence in wet tropical environments (particularly scat).
- (3) Sign clustering (e.g. extensive termite digs), which creates difficulties for interpreting, for example, how many individual bears may have generated the sign.
- (4) Observer bias and fallibility in sign detection.
- (5) Sample size limitations of genetic samples for bear home ranges, overlap, and relative density data.
- (6) Habitat bias (e.g. masking of sign age or the conundrum that sign presence may indicate either habitat use or the ability of that particular habitat type to reveal certain bear signs better than other habitats confounding sign absence or masking).
- (7) Equal access by bears to habitats within each site.
- (8) Hunting removal of individuals from the area, which may confound sign and density estimates relative to different habitats, particularly where human access is greatest.

With all of these issues, the burden of this study was to generate a reasonable assurance that sign absence actually meant avoidance of specific habitat types or resources, rather than the case that presence indicated selection of specific habitats or resources by a certain number of individuals. These concerns were addressed by:

- (1) Randomised sampling designs and modelling protocols to account for variability in sign detection from habitat bias, limited sign persistence, survey period, variability in bear behaviour, and so forth.
- (2) Employing a diversity of sampling and analysis methods, including a two-staged nested experimental design, grouped data, several different statistical procedures, and detection, occupancy, and diversity modelling (Chapters 5 and 6).
- (3) Maximising sample sizes.

- (4) Replicating censuses within habitats, disturbances, seasons and years.
- (5) Testing the efficacies of different sampling methods through significance tests with verified data.
- (6) Pooling data from multiple years to reduce the effect of random year-to-year fluctuations in habitat use and sign delectability.
- (7) Pooling annual data to reduce seasonal effects of variation in sign density and bear behaviour.
- (8) Using a strategy of method redundancy (i.e. Distance sampling, Fixed-width sampling, camera-trapping, and genetic sampling) in the same and different sites and periods (*see* Chapters 5 and 6).

CHAPTER 5

SUN BEAR ECOLOGY, HABITAT, AND LANDSCAPE USE



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SIGN AND BIOGEOGRAPHIC SURVEYS

PRELIMINARY STUDY

Military activity by both Free Aceh Movement (GAM) and government forces increased in intensity between June and December 2001. By December 2001, the Leuser Management Unit and local government were obliged to close the Ketambe research station and all other stations in Aceh to non-Acehenese citizens. Only essential Acehenese maintenance staff were asked to remain. As a result, surveys for the current project ended at Ketambe by November 2001 and all Leuser Ecosystem surveys were then based in North Sumatra from the Elephant Patrol Unit (UPG) of the Leuser Management Unit in Aras Napal.

5.1 Preliminary Research

Feasibility results from 1998 and 2000 showed that sign surveys were effective and could be conducted by trained staff. Thus, the full-study began on 3 September 2001 at the Ketambe research station in Aceh, Sumatra. Preliminary research entailed a two-month study to test and finalise methods, more extensively test sign and habitat bias, and train local field assistants. A total of 24 km of transects (1,000 x 10 m each) were conducted from 3 September – 30 October 2001 using Fixed-width censusing (10 m width) and Distance (line-transect) sampling protocols (*see* section 5.2). Survey sites included a diverse array of habitats at elevations of 252– 1,010 m asl in primary undisturbed forest, secondary forest (1 – 15 years old), subsistence gardens, large cash-crop gardens, trail systems, and clear-cuts.

5.1a Sign Aging and Habitat Biases

An important aspect of this preliminary work was testing and examining more detailed aspects of habitat biases. Potential habitat biases of particular sun bear signs were tested by:

- (1) Simulating claw marks, termite diggings, tracks, log tearing, and so forth with random tree species, soils, elevations, slopes, and aspects in isolation from, and adjacent to, actual bear signs in representative habitats.
- (2) Comparing the aging process of the known and simulated signs.
- (3) Testing field assistant knowledge and skills with sign identification and age estimation.

During this preliminary work, I simulated claw marks with a machete on 25 random tree species (n=25 trees) in primary forests, edge forests, forest gaps, and open areas. These test-signs were made to represent different bear size/age classes (cubs to large adults) by varying the depths, weighting, angles, and sizes of the claw marks. In some cases, simulated claw marks were made on the same tree adjacent to actual sun bear claw marks. Trees were examined every 3 - 5 days for signs of aging, including cambium and inner-wood deterioration, colour changing, bark and inner-wood growth, bark peeling, and so forth, and were compared with actual bear signs. To estimate claw mark signs older than 1 - 2 years, logged trees with claw marks were studied. In these cases, the time logging occurred was known and, thus, the minimum ages of the claw marks were known and could be compared for aging on dead trees relative to fresh marks. In primary forest, claw marks on fallen trees were aged in a similar fashion. During their other work over the years, local assistants marked many live and dead trees with machetes to provide travel directions or other practical needs in the forest. Because the exact ages of these marks were known, they were aged and compared on live or dead trees with our simulated test-signs.

For ground-based signs like tracks and diggings, tests were conducted in various substrates and studied in 24 hour periods over two months. Cues, such as the moisture content of overturned or depressed soil, exposure to sunlight and rain, degree of litter fall covering the sign, and so on were assessed. Tests of prints from dogs and people were used and were good for calibration. Sign aging of other species were also used as tests and were validated by sightings and then back-tracking the tracks, claw marks, diggings, discarded food, and other signs. These latter events occurred at random in various substrates and were then examined for type, character, and aging over the course of the two month preliminary study. These species included and were not limited to: pigs, deer, civets, binturong, pangolin, tigers and smaller felids, elephants, squirrels, shrews, marten, orang-utan, langurs, macaques, porcupine, and frugivorous birds. Training in species other than sun bears was important for (a) general experience and understanding of animal signs, (b) calibrating bear signs, and (c) developing a knowledge base for the presence-absence of competing and antagonistic species of sun bears.

5.1b Field Assistants

Local knowledge has been vastly under-estimated and is most often unused in ecological research. This knowledge-base is highly relevant, extensive, and deserves serious respect and consideration. All local assistants on this study were life-long forest dwellers and workers in these study areas and only those with particular knowledge in the study sites and wildlife ecology were employed. This was especially the case with the project's Dayak assistants in East Kalimantan, whose daily subsistence depends critically on their intimate knowledge of forest dynamics and animal ecology, signs, and behaviour. These assistants have life-long ecological and animal behaviour knowledge in these study sites, know the number of people using particular areas in specific periods and for what purposes, and know where, when and how the study areas were disturbed, including the timing of particular trees being cut. Generations of this accumulated knowledge was principally embodied in the Kepala Adat (Head of Traditional Knowledge of the upper Bahau River region) who worked as our lead assistant in East Kalimantan. I appreciated and learned a great deal from these assistants and project success was due in large part to their knowledge, skills, and hard work.

Only Indonesian nationals were trained and employed on this project. Providing technical training and leadership education in conservation and science for local Indonesians proved very successful throughout this project. More than 65 Indonesians were trained and worked on this project and joint projects with my local collaborating organisations.

Inter-regional and cross-cultural training enabled individuals from diverse backgrounds, skills, ethnicities, cultures, education levels, and religions within Indonesia to improve professional networking, education, team-building, and knowledge of other ecosystems and regions within their own country. Thus, lead assistants from Sumatra were flown to Kalimantan in 2002 and 2003. By enabling these men to work between areas, their training continued, which helped improve their professional development and education. This also provided opportunities for potential career advancement by enabling them to network with the project's other collaborating organizations and to share their knowledge with other Indonesians.

Scientifically, this inter-regional skill-sharing and training provided method and worker consistency for the project across field sites. This greatly aided the research, provided key knowledge of Sumatran ecosystems as an important base and comparison in Borneo and *vice versa*, improved partnerships among colleagues with common goals, enhanced efficiency among members of the team who had long-term experience working together, and minimised very costly delays by reducing the many months of training necessary for new assistants.

5.1c Biogeographic Data

Field assistants were trained in biogeographic sampling methods, for which the data were recorded in each 10 x 10 m sub-section along every transect (table 5.1). Further details are in the Habitat Assessment section of this chapter. Slope and tree height were calculated using (a) the angle meter provided on compasses and (b) back-pacing and calculating tree height based on distance and angle to the tree crown. Aspect was recorded using a compass and elevation with an altimeter. GPS (Global Positioning System) locations were acquired with Garmin 12 XL hand-held units (Garmin 2001).

Table 5.1. Biogeographic data recorded for each 10×10 m sub-section on every transect. These data categories were tested and validated during field trials in 1998, 2000, and 2001 and were used on all subsequent transects through the end of the study.

Canopy Cover (%)	Habitat Type and Characteristics
Ground Cover (%)	Forage Cover $(0-4)$
Slope (degrees)	Basic Available Forage (0,1)
Aspect	* Fruit
Elevation (m)	* Termite & Ant Colonies
Distance to Water Source (m)	* Bee Hives
Predator Presence (0,1)	* Tubers, Mushrooms, Plants
Competitor Presence $(0,1)$	* Other Forage
Other Species of Concern	Habitat Disturbance $(0 - 4) + (Type, Age, Distance, Extent)$
Refugia (escape cover) $(0-4)$	Human Activity $(0-3) + (Type, Age, Distance)$

Biogeographic Data Recorded for Each 10 x 10 m Segment of All Transects

Canopy cover was estimated using a densitometer (GRS 2001) that was graduated into four equal sections representing 25, 50, 75, and 100% canopy cover of the 10 x 10 m transect sub-section. According to Graphic Resource Solutions (2001), a cover estimate with this densitometer based on a sample of 100 points yields a 95% confidence interval between $\pm 6.0 - 10.1\%$ cover. An estimate based on 200 points produces a 95% confidence interval of $\pm 4.3 - 7.1\%$ cover. At least 1 reading/10m sub-section was taken on every transect, producing a minimum of 100 readings/transect.

Ground cover was defined as the horizontal coverage of shrub, plant, seedling, and sapling growth < 1.5 m tall. Coverage was estimated by inverting the densitometer at a 90^o angle to the canopy and estimating horizontal cover across the 10 x 10 m sub-section. Escape (security) cover, or "Refugia", was defined by the number and availability of mature trees > 20 cm dbh along with the degrees of canopy cover, ground cover, rocky out-crops, riparian

zones, gullies, and steep ridges for escape. Refugia cover was calibrated on a scale of 0 - 4 representing the percent geographic coverage in 25% increments in the 10 x 10 m subsection, such that 4 = minimum of 2 - 3 mature trees > 20 cm dbh plus ≥ 90% canopy cover and > 20% ground cover available within 10 m. No refugia (e.g. clear-cut) = 0.

Basic forage was counted in the $10 \ge 10$ m sub-section for each unique food item, which was scored with 1 and summed at the end of each 100 m section. Forage, such as all of the fruit on a single tree or all parts of a termite colony, was considered one item. Basic forage cover was estimated as the geographic extent of that item as described in the Habitat Assessments section of this chapter.

The types, ages, distances, and extent of habitat disturbance and human activities were recorded. This effect was measured by a scale of 0 - 3, where 0 = no human presence, 1 is ≤ 25 people present/week, 2 is 26 - 50 people present/week, and 3 is > 50 people present/week. The type of activity (e.g. hunting, gathering, farming, trail transit, river traffic, etc.), age of, and distance to these activities were recorded.

The types, ages, intensities, and geographic extent of habitat disturbance can also influence animal movements, behaviour and ecology. Thus, disturbance intensity was based on a scale of 0 - 4, where 0 = no disturbance and 1 = 1 - 25%, 2 = 26 - 50%, 3 = 51 - 75%, or 4 = 76 - 100% respectively, of the amount of the original area disturbed. For example, one tree cut for gaharu in which > 95% of the original habitat remains was level 1, whereas cleared forest in which < 25% of the original habitat remains was level 4. Extent was based on the actual geographic coverage (m²) of disturbed area, including surrounding damage from felled trees. Disturbance types included logging, agriculture, trails, roads, villages, and so forth along with their after-effects as, say, secondary growth in variously aged stands that no longer retained original forest character. Ages were calculated on a monthly scale, such that 1 day old = 0.03 months, one week = 0.23 months, one year = 12 months, and so on.

5.1d Bear Signs

Data recorded for all bear signs encountered are noted in table 5.2. Basic information on the habitat type (e.g. primary forest, swamp, montane forest, etc.), micro-habitat characteristics (e.g. riparian zone, rocky outcrop, forest gap, etc.), canopy and ground covers, and topography were recorded. The type of sign was recorded along with whether we were at least 95% certain the sign was made by sun bear, noted as 1 or 0. Sign age and its exact location to the metre along the transect and distance from the transect centre line were also noted. Where possible, the relative size class of the bear (i.e. cub, medium-sized adult, large adult) was estimated based on, for example, the size and weighted depth of claw marks

or prints. All standard measurements were also recorded for complete claw marks and prints, including the width between the center of the first and fifth digits for both claw marks and prints. If the signs were claw marks on a tree, basic information on the tree such as its height, circumference, and species were noted. Tree circumference was the best measure in the field for Indonesian field assistants unfamiliar with dbh tape measures. Diameter at breast height (dbh) was converted later using the common equation from Euclidean geometry:

diameter = $\frac{circumference}{\pi}$

The bear's activity level was gauged on a 1-5 point scale of low to high intensity to denote the relative degree of habitat or resource use. This scale was graduated as:

- 5 = intensive use or multiple visits of the same age and same size class bear (if measurable) indicated by signs, such as (a) multiple climbs with assocaited foraging, nesting, etc, (b) extensive termite digging(s), where > 50% of the visible colony was excavated at the same time; (c) nest building or dens; (d) torn-opened trees for bee hives, termites, grubs, ants, and other insects.
- 4 = signs, such as climbing trees for prolonged fruit foraging of one bout or termite colony excavations of < 50% of the colony, and so forth.
- 3 = signs such as single event tree climbing for unknown or exploratory reasons or partially torn logs for termites and other insects, and so forth.
- 2 = signs such as typical Ursidae territorial markings, minor earth digs, and so forth.

1 = signs, such as tracks, scat or hair, which may only indicate travel through the area.

Table 5.2. Data recorded for all sun bear signs encountered along each transect. These data categories were tested and validated during field trials in 1998, 2000, and 2001 and were used on all subsequent transects through the end of the study.

Data Recorded for All Sun Bear Signs Encountered			
Sign Type	Canopy Cover (%)		
Sign Verification (0,1)	Ground Cover (%)		
Multiple Use (0,1)	Slope (degrees)		
Sign Age (months)	Aspect		
Bear Size / Age Class	Elevation (m)		
Activity Level $(1-5)$	Disturbance $(0-4)$		
Habitat Type	Human Activity $(0-3)$		
Sign Tree Circumference (cm)	Distance to Transect Centre		
Sign Tree Height (m)	Exact Location on Transect		
Sign Tree Species	Distance from Start (m)		
Micro-habitat characteristics	Section #		

5.1e Field Assistant Testing

All simulated and test-sign ages, tree heights, canopy covers, slope angles, and so forth were only known to me and, thus, field assistants were trained and tested randomly at different times and locations throughout the study. In some cases, simulated signs were placed adjacent to actual bear signs and assistants were tested in a double-blind test during actual surveys. In the first week, correct estimates and calculations for signs were > 95% and for field methods were about 78%, but by the end of the second week success rates for the latter rose to a mean of about 90% and by the end of the first three weeks accuracy was > 96% for sign, ecological and methods knowledge. Based on these results, it was assumed that method consistency and accuracy were achieved. Nevertheless, some habitat biases as well as human error and biases are unavoidable. Thus, constant testing and study of various potential biases continued on a systematic basis throughout the full-time study at all sites.

5.1f Preliminary Survey Results

Variable transformations and statistical analyses for the Ketambe 2001 preliminary data were run in SYSTAT version 10 (SPSS 2000). Results of the 24 transects showed that sun bear sign frequencies (square-root transformed) were significantly different among habitat types by both ANOVA (F=3.23, df=3, P<0.0001) and non-parametric Kruskal-Wallis tests (X²=434.0, df=3, P<0.0001). Mean sign age was 1.9 years old and the majority of signs were located in undisturbed primary forest at a mean elevation of 492 m asl on slopes of about 18° with > 92.3% canopy cover, high escape cover (\geq level 3.33), and moderate ground cover < 25%. Areas with significantly less sign had canopy covers < 65%, escape covers ≤ 2 , and high ground covers > 30 - 50%. Availability of fruit and total forage cover appeared as potentially important effects in a general linear model (GLM), but the most notable effects were from disturbance differences among survey sites (adjusted $r^2=0.954$, F=130.03, df=68, P<0.0001). Although the sample size was relatively small (n=24 transects) these preliminary study results combined with those of the feasibility study (n=14 transects) comprised 38 km of transects in multiple habitat types and sites on Borneo and Sumtra, providing adequate tests and refinement of methods and presented sufficient confidence to begin the full study.

FULL STUDY

Objective 1: Sun Bear Ecology, Habitat, and Landscape Use

5.2 Bear Sign Surveys

5.2a Fixed-Width Transect Censuses

To ensure a representative sample of ecological conditions and habitats, focal areas were selected *a priori* based on known ecological and topographic features, habitat type, elevation, proximity to and types of disturbances, government permits, accessibility, and location of research facilities. Rebel activity in Aceh limited focal areas to North Sumatra. Surveys were conducted on Sumatra and Borneo simultaneously by multiple teams.

A stratified-random study design was used for transect locations. Depending on the focal area and map availability, a 1 or 2 km² grid was first overlaid on topographic maps and, where available, habitat classification maps derived from existing GIS data layers, the latest TM 10 m panchrome data from Landsat 7, or aerial photographs. A stratified random sample of survey sites was then selected within each focal area, such that 48 km² sites were randomly delineated to encompass a representative sample of habitat and disturbance types, including disturbed and undisturbed areas with and without hunting, with varying topographic and biogeographic features within each grid cell. In some cases the extent of available survey area was limited to sites < 48 km². Because randomisation procedures provide robust statistical power (Ott 1988, Ott and Longnecker 2001), at least one to two 1,000 m transects were randomly assigned to each grid cell. Each transect and grid cell was numbered using a random numbers table and a 50% random sample per site was selected to satisfy minimum random sample sizes of > 20 per site (Ott 1988).

In some tropical systems reduced transect widths in thick vegetation are necessary to ensure adequate survey reliability (Garshelis *et al.* 1999). Such transects have been as narrow as 4 - 5 m and can be conducted by two people (Gibson and Hamilton 1983, Augeri and Pierce 1996, 1997). Preliminary work indicated that a transect width of 10 m in these areas is optimum when surveyed by three people (Augeri 1999, 2000). Thus, three-person teams conducted systematic censuses along fixed-width transects (1,000 x 10 m) where two trained field assistants were spaced 2.5 m on either side of the centre line, while I or a lead assistant surveyed from the centre line out to 2.5 m. The direction of each transect was determined by a random compass bearing directed in a straight line. In some cases, slope contours needed to be followed. Within a study area, minimum distances between transects were > 1,000 m with \ge 80% more than 2,000 m apart, while semi-replicates were 250 – 500 m apart (described below). If random compass bearings indicated crossing other transects, new bearings were used. All transect lengths were measured with a hip-chain to 0.1 m accuracy using 2,500 m spools of biodegradable string and the beginning and ends of each transect were marked with GPS acquired coordinates. All transects were subdivided into ten 100 m survey units (figure 5.1) for further statistical tests (*see* section 4.7 for sample sizes) and for habitat and tree stand surveys. Each 100 m section was marked with florescent coloured flagging ribbon and numbered 0 – 9. All 100 m sections were further sub-divided, but unmarked, into ten 10 m sub-sections for micro-habitat and forage surveys (figure 5.1).

Systematic censussing for independent bear sign events was conducted based on all known indicators, such as sightings, scat, claw-marked trees, termite diggings, torn logs, food deposits (e.g. discarded fruit, bee hive or termite colony pieces, etc.), day beds, spoor, hair, and "dens" (figure 5.2). One bear can create numerous signs in the same period and area, so distinguishing independent sign events and their ages was critical for determining habitat use and occupancy relative to specific biogeographic or anthropogenic effects. Criteria used to identify independent sign events were (1) sign age, (2) sign type, (3) sign extent (e.g. excavation of one termite colony could cover several square metres and may be considered one sign if age could not be verified, whereas diggings of different age or obviously different colonies that are clearly geographically separated were considered distinct signs), (4) relative size/age class of the bear generating the sign (e.g. cub *vs.* adult), and (5) exact location along the transect relative to other sign. In some cases, the same termite colony or bee hive was excavated or a tree was climbed more than once. In these instances, sign age and relative size/age class of the bear were the most important distinguishing features.



Figure 5.1. Fixed-width transect design. All transects were $1,000 \ge 10$ m and were divided into ten 100 m sections. Each 100 m section was divided into ten 10 m sub-sections.



Figure 5.2. Examples of positively identified bear sign. From top row: Tree torn-open for bee hive; claw marks; spoor; log torn-open for termites; scat.

Census protocol was: workers on either side of the centre-line followed a modified Adjusted Angle Zig-Zag Sampling Design (Thomas *et al.* 2003) with a sinusoidal search pattern (Anderson *et al.* 2001, Buckland *et al.* 2001), conducted at < 0.13 km/hour back and forth from the centre line to > 5 m out. The central observer maintained the straight-line compass bearing, recorded all information, and searched 0 - 2.5 m on either side of the centre line (Buckland *et al.* 2001). Data categories recorded for all independent signs encountered were tested and validated during field trials in 1998, 2000, and 2001 and are noted in table 5.2. On some transects bear claw marks were observed on roots, branches, on a side of the tree opposite the observer, and on trees as small as 5 - 6 cm dbh. Hence, all parts of all trees and saplings within the 10 m wide strip were surveyed from ground to crown. Habitat information (table 5.1) was tested and validated during field trials in 1998, 2000, and 2001 and was thus recorded every 10 m along all transects to examine potential habitat correlations with bear use (section 5.6). Where possible, photographs of particular signs were taken for more detailed analyses and/or for comparison with other signs and sites. The exact location of each sign along the transect was recorded to the metre.

Use of trained scat-detecting dogs was originally proposed to, and approved by, the Indonesian host institutions and Indonesian Institute of Sciences in 1999. This method is tested to be highly effective for locating scat from bear and other species (Wasser *et al.* 1999, 2004) and was intended to increase scat and hair discoveries during surveys. By 2001, government changes resulted in permit denial and dogs were not used.

Randomised sampling periods decrease selection bias and, thus, transects were conducted during random periods within each season to coincide with seasonal changes in bear food selection and behaviour (Garshelis 1991). Whenever possible, an equal number of transects were conducted across sites. Study design followed randomisation theory and minimum sample sizes of $n \ge 25$ transects were achieved in most areas. In some cases with limited geographic area, it was not possible to conduct 25 or more transects at some sites, but additional transects were done in the same habitat types at other sites to maintain sample sizes at appropriate levels. Further details of sample sizes are discussed in section 4.7.

Parallel and perpendicular replicates were conducted randomly for transects within the same habitat blocks, but replicate censuses were not done on the same transects. Repeating the same transects was not effective for this study due to: (A) possible redundant counts of sign(s). (B) Known wild sun bear home ranges at the time of this study were $4 - 20.6 \text{ km}^2$ (Wong 2002, Meijaard *et al.* 2005) and surveys limited to repeated censuses of the same 1,000 m transect would not provide appropriate geographic coverage within one or more bear's range(s). (C) Repeated surveys on the same transect limit sample size coverage of representative habitats and biogeographic conditions that may influence bear movement patterns across the landscape. These and other factors associated with redundant sign counts confound estimates of sign density and abundance, including for Distance sampling methods (*see* proceeding section: Distance Sampling), along with site-occupancy modelling and analysis of sign as indices of occupancy and habitat use. Both scientific and ecological accuracies were improved by conducting semi-replicate surveys *via* perpendicular and parallel transects 250 - 500 m apart within the same habitats and conditions.

Resulting data were used to estimate presence-absence, occupancy, and relative sun bear habitat use and distributions among habitat and disturbance types. It is important to emphasise that these sign suveys were *not* used to estimate bear population abundances or densities, but rather for relative abundances and densities of distinct bear sign events or objects along a transect as a gauge of relative habitat use. Densities and distributions of sun bear signs via Fixed-width sampling were estimated by comparing the densities and distributions of signs from transects in similar habitat types and environmental conditions (Garshelis *et al.* 1999), where the frequencies of each bear sign were recorded per unit area for each transect.

5.2b Assumptions

The primary assumption of Fixed-width transect surveying is that all signs within the fixed transect area are observed. Violations of this assumption were minimised by searching all parts (ground to crown) of every tree within the survey strip and between trees the ground, undergrowth, and all portions of the strip were searched systematically at a measured pace < 0.15 km/hour in a zig-zag search pattern.

The density (D) of bear signs/transect was calculated by the following equation:

$$D = \frac{n}{LW}$$

where n is the number of distinct sign events or objects, L is transect length, and W is transect width. Differences in relative bear sign densities and abundances among habitat types, biogeographic conditions, and disturbances were analysed with statistical designs and modelling outlined in Chapter 6.

5.2c Distance (Line-transect) Sampling Surveys

A modified version of the Distance (Line-transect) sampling method (Burnham *et al.* 1980, Buckland *et al.* 1993, 2001) following Anderson *et al.* (2001) was used for the same

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transects outlined above. In general, this method is more statistically rigorous than standard Fixed-width transect censuses, particularly in Tropical forests where the probability of 100% sign detection is low due to habitat and environmental conditions While it is assumed that all objects within a fixed-width transect are observed, the Distance-sampling method surveys a *sample* of the object population by using count and distance data to estimate detection probabilities of focal objects or animals in different habitat types, time periods, distances, and so forth. Models then correct for potential bias and variability, estimate potential missed objects or animals, and derive abundance and density estimates of the object or animals. It is stressed that Distance-sampling methods were used to estimate densities, abundances, and detection probabilities of bear signs rather than animals. This method is designed for situations like this study, where the detection of inanimate objects within the sample area is not certain and varies between objects in different habitats and seasons (Buckland *et al.* 1993, 2001). Accordingly, Distance sampling was used to test, corroborate and verify sign sampling techniques in general and relative to Fixed-width sampling protocols.

The Distance-sampling method applied in this project used the same systematic survey techniques on the transects as described above for Fixed-width transects, including the Adjusted Angle Zig-Zag Sampling Design (Thomas *et al.* 2003) with sinusoidal search pattern (Anderson *et al.* 2001, Buckland *et al.* 2001). The only additions were searches extended 0 - 25 m from centre and the perpendicular distance from the centre line to each independent bear sign detected were recorded in centimetres (figure 5.3). A key assumption is all objects that are on the centre line are detected, but as distance increases away from the line, detectability decreases (Wilson *et al.* 1996, Buckland *et al.* 1993, 2001). Preliminary study results indicated that this remains true for sun bear signs (Augeri 2000, 2001).



Figure 5.3. Distance (Line-transect) sampling design. All transects were 1,000 m long and were divided into ten 100 m sections. Each 100 m section was further divided into ten 10 m sub-sections. Wherever bear signs were encountered, the perpendicular distance from the sign to the centre line was recorded in centimetres.

This study differed in one important manner from those studies for which Distance sampling can be optimally applied: the nature and type of sun bear signs. Most wildlife Chapter 5

studies using Distance-sampling techniques survey for relatively detectable animals or objects that can be sighted at varied distances. This even includes elusive birds, primates, and other species in dense tropical forests, which first can be detected from calls and movement sounds. Sun bear signs, however, are different. While there are very obvious signs like termite digging that can be detected from larger distances, other signs like spoor, scat, and claw marks on trees are not always readily detectable (Augeri 1999, G. Fredriksson pers. comm.). Even though some claw marks can be seen from a greater distance, at times they may be hidden behind branches, shrubs, or on opposite sides of the trees from where the observer is searching. Thus, systematic sinusoidal census protocols (Anderson *et al.* 2001, Buckland *et al.* 2001), in conjunction with Distance-sampling methods, were highly effective for conducting these surveys and to test Fixed-width sampling methods. Search effort was more comprehensive and Distance sampling generated more robust probabilities of missed objects and sign density and abundance estimates for occupancy and distribution modelling.

There are many similarities between Fixed-width and Distance methods, including surveying inanimate and cryptic objects (e.g. nests, insects, plants, animal signs), *a priori* distance or transect width limits, assumed 100% detection along the centre line, and randomised designs (Buckland *et al.* 1993, 2001). Thus, Distance-sampling methods were applied within the censussed transects as an additional measure of sign abundance for a more rigorous estimate of any differences in the bear's relative habitat use.

In order to test this assumption and the applicability of this modified method before the full-time study, preliminary sign census data from Augeri (2001) were tested using this approach in program DISTANCE (Thomas et al. 2003). Buckland et al. (1993, 2001) suggest that an *a priori* distance limit in the field can be established for surveys, beyond which observations are ignored. This can also be accomplished in analyses via truncation where outliers are ignored. Buckland *et al.* (1993, 2001) recommended a standard 5 - 10%truncation in analyses to decrease variance and generate a more robust estimate for the probability (p) of detecting an object at a distance from the transect centre line. The probability detection function on the centre line is g(x) with an assumed 100% probability of detecting objects on the centre line, such that g(0) = 1. This function is identical in graphed shape to the probability density function f(x) of objects detected at 0 perpendicular distance from the centre line. Results of preliminary data showed that truncation reduced bias in the density estimate, D, and increased precision. In the preliminary field censuses, maximum observed distances from the centre line in either direction were 15 - 20 m, with an average maximum distance of about 17.2 m. Thus, a 10% truncation at 15 m from the centre line was used for these analyses.

Preliminary survey data tests in programme DISTANCE with a truncation at 15 m produced a high Chi-square goodness of fit probability ($X^2 p = 0.97758$) under the Halfnormal Cosine model and a high probability density function (f(0) = 0.64803) with non-parametric bootstrap (100 repetitions) variance at a 95% confidence interval. The graphed shape of the detection function also produced a good right shoulder without spiking at 0. The probability of detecting a sign event or object on a transect was p = 0.34292. Without truncation, which is appropriate for a fixed-width area, p = 0.58954. Under the Hazard Rate Cosine model and Poisson distribution, p increased to 0.76784 and without truncation p = 0.81929, both of which were closer fits to the actual distribution of bear signs in the forest.

Buckland *et al.* (1993, 2001) demonstrated that the Hazard Rate model is designed for studies such as this, where there are less than optimal conditions for detecting objects. This model was also particularly useful due to the nature of inanimate objects (e.g. bear sign) and because it inherently possesses robust properties while fitting genuinely spiked data well (Buckland *et al.* 1993). It is derived from *a priori* assumptions for the detection process, as in this project, where it is assumed bear signs are difficult to detect and may be randomly distributed due to biogeographic characteristics.

Considering the positive results from preliminary data from 2000 and 2001 (n=35 transects), this method was applied to the more extensive present study. Thus, in addition to analyses from Fixed-width transect censuses, a distance function was fitted to all observed bear sign events or objects using the software programme DISTANCE (Thomas *et al.* 2003). This method enabled more robust estimates of (**a**) the proportion of signs missed along the transect and (**b**) bear sign abundances and densities. Differences in relative bear sign densities and abundances among habitat types, biogeographic conditions, and disturbances were then modelled and examined using the statistical scheme outlined at the end of this chapter.

Given the high degree of variance between sites, sign data were transformed using square-root or log-based transformations in SAS (SAS 2002). Differences in bear sign frequencies relative to independent variables, such as fruit productivity, tree stand characteristics, disturbance, and so forth, were examined by General Linear Model (GLM) analyses, as described in the statistical scheme discussed in section 5.7.

5.2d Assumptions

The DISTANCE software programme (Thomas *et al.* 2003) enabled analyses for some of the inherent limitations of this study, such as variance between habitat types and seasons, stratification, and clustering of sign. This program also accounts for issues such as a

detection probability on the line g(x) < 1, due to problems like limited sign persistence in tropical environments. Wilson *et al.* (1996) noted four assumptions critical for this modelling are:

- (1) Animals or objects directly on the transect line are never missed.
- (2) Animals or objects are detected at their initial location prior to any movement in response to the observer and are not counted twice.
- (3) Distances and angles are measured accurately.
- (4) Detections are independent events.

For this study, the framework for detecting bear signs rather than actual bears, and the fact that all transects were only conducted once in one direction by the same observers to avoid redundant and concurrent counts, automatically negates assumption two. Bear distributions were unknown and placement of transects was under a stratified-random design independent of bear distribution. Surveys were separated by > 1 km for the majority of transects and > 250 - 500 m for random parallel or perpendicular replicates and each detection of a distinct sign event was independent of others. This independence of both transects and detections minimised violation of assumption four. All sign events were measured at a perpendicular angle to the transect centre line and distance measurements were recorded with standard metal retractable tape-measures. These methods were standardised and tested in the preliminary work and were found to be accurate at > 95%. Thus, assumption three was minimised (Wilson *et al.* 1996).

The only possible violation of these assumptions in this study was that sign objects could be missed along the transect centre line, which will produce overestimation of g(0) and consequent underestimated density and abundance counts. Wilson *et al.* (1996) noted this violation most likely occurs when the observer and target animals are on different horizontal planes (e.g. when surveying for bird or fossorial species), but this can be avoided with trained multiple observers who have a well-developed search image of the target object (Wilson *et al.* 1996). Because three trained and experienced observers per transect surveyed for signs occurring within their same horizontal plane, violating this assumption was reduced. Nevertheless, due to the cryptic nature of some bear sign objects, there is always a probability that some signs were undetected. DISTANCE modelling software accounts for this inherent violation by calculating a detection probability and estimation of missed objects. These are primary reasons for using this sampling method and software and, thus, violation of this assumption was minimised.

5.3 Detection Probabilities

Predicting whether or not an animal is consistently occupying an area is critical for understanding densities, distributions, and population sizes. These occupancy estimates (ψ) are a direct function of detection probabilities (Buckland *et al.* 2001, MacKenzie *et al.* 2002, Royle and Nichols 2003), such that the probability (*p*) that any given sign is detected will determine the probability that a site is consistently occupied by that species (MacKenzie *et al.* 2002, 2003). For indirect surveying, such as presence-absence data by sign censuses or camera-trapping (Chapter 6), these probabilities provide a rigorous method for estimating animal density and abundance (MacKenzie *et al.* 2002, 2003, Royle and Nichols 2003).

It can be assumed that different habitat types will bias the probability that signs are detected (Garshelis 2000). This remains true for sun bears, where different tree species, substrates, bear sizes, and so forth may affect the detectability of various signs. Randomisation Theory (Ott 1988, Ott and Longnecker 2001) suggests that ample sample sizes (n > 25) of randomly-distributed surveys minimize possible bias. Multiple surveys in representative habitat types increase the accuracy and precision of detection and enable predictions of whether an animal is consistently occupying an area, as well as the proportion of area occupied, even when detection probabilities are < 1 (MacKenzie *et al.* 2002).

MacKenzie *et al.* (2002) developed a model for estimating the site occupancy probability (ψ) for focal species where the species may not be detected even when present at the site. The model is based on a probability equation of presence-absence data (more appropriately considered here as detection-non-detection) to describe the observed detection history for a site over a series of surveys. For example, the probability of detecting a species in the first, second, and fourth surveys of the site is represented by the detection history: 1101, which is estimated by the equation:

$$\psi \times ((p[1])(p[2])(1-p[3])(p[4]))$$

According to MacKenzie *et al.* (2002), the probability of never detecting the species at that same site would be a detection history of: 0000, with a probability of:

$$\psi \times ((1 - p[1])(1 - p[2])(1 - p[3])(1 - p[4]) + (1 - \psi))$$

In the case where there may be lack of detection, the species might have either been absent from the site $(1 - \psi)$ or was actually there but was never detected. Hines (2005) notes that

by combining these probabilistic statements for n sites, maximum likelihood estimates of the model parameters are achieved.

Detection probabilities were estimated separately for sign survey and camera trapping data (Chapter 6) using the MacKenzie *et al.* (2002) models in programme PRESENCE version 2.05 (Hines 2005). Camera trapping was used to validate presence for sign surveys (Chapter 6). Estimate precision depends on accuracy in the field, such that identification of independent sign events is maximised (section 5.2a). A major element for sign-surveying analyses as presence-absence data is also defining the sampling occasion. The data matrix in PRESENCE is based on (sites) x (sampling occasions) and, thus, transects were analysed as different survey "plots" in a study area and the 100 m sub-sections were modelled as semi-replicate sampling units of each transect plot, which provided a measure of intra-plot variability (Williams *et al.* 2002). Given the randomised-sampling design and because inanimate objects were censused rather than live animals that can move and influence counts, the actual sampling time was irrelevant. Thus, sub-sections could be modelled as semi-replicate surveys of a plot, which satisfied most independence issues in this respect (Williams *et al.* 2002). Nevertheless, section independence was tested by two-way Chi-square tests of sign clustering at 10 m, 100 m, and 200 m resolutions (section 6.4).

Standard detection-non-detection histories were created in Excel spreadsheet pivot tables for sign survey and camera trapping data for each site. Because the Royle and Nichols (2003) model accounts for abundance heterogeneity, all capture histories were analysed as both presence-absence series data (1, 0) and actual count data. For presence-absence, if there was ≥ 1 independent event/100 m section or trap site, it was recorded as "1". No event was recorded as "0". Each data-set was analysed in programme PRESENCE as a single season model and all optional models were run, including single and multiple group models with either constant or survey-specific *p* as well as the abundance-induced heterogeneity model by Royle and Nichols (2003). PRESENCE computes several between-model and goodness-of-fit test statistics to estimate model suitability, and the log-likelihood function (Akaike's Information Criteria (AIC)) was used for objective selection of the most appropriate model.

5.3a Assumptions

An important assumption for detection probabilities in the MacKenzie *et al.* (2002) model is that occupancy of a site does not change during surveying. For sighting surveys, this may be violated by species with large home ranges, where the animal may be in other portions of its range during the surveying (Hines 2005). For sign surveys, this assumption generally does not apply because the sign(s) will be present even if the animal is not there.

Potential violation of sign presence occurs at temporal scales of analyses, i.e. depending on when occupancy is defined relative to sign age. If temporary absence from the site during sighting or camera trapping surveys is due to random events or behaviour, then violation of this assumption is also insignificant (MacKenzie *et al.* 2002, Hines 2005). The model assumes that the sites are closed at the species level rather than at the individual level. Thus, movement of individuals between sites does not affect the model (MacKenzie *et al.* 2002, Hines 2005). In either case, estimated occupancy needs to be interpreted as "use". One particular violation of the closure assumption in traditional capture-recapture models is that of transient animals passing through the study area. This potential violation was accounted for in the MacKenzie *et al.* (2002) model, which is only closed at the species level and allows for transient animals.

If detection probabilities are not directly related to the probability that a site is occupied, unmodelled heterogeneity in occupancy probabilities might be closer to an average level of occupancy. This is an important assumption, for which it is assumed that parameters are constant across the sites surveyed. Failure creates heterogeneity. Due to environmental and behavioural factors, heterogeneity exists naturally in most detection probabilities, but the most important source of such variance is animal abundance. Royle and Nichols (2003) demonstrated the direct link between detection probability and animal abundance (N), where variability in N will trigger heterogeneity in site-specific detection probabilities. Consequently, the probability distribution of abundance is estimated as a direct consequence of the detection probability, such that p increases as the number of animals increases (Royle and Nichols 2003). With satisfactory probabilities and variance, this method has positive applications for presence-absence data as an index and, in some cases, estimate for animal abundance (MacKenzie *et al.* 2002, 2003, Royle and Nichols 2003).

Perhaps the most important assumption of the model is that surveys are independent with a Poisson or random distribution. As discussed in the previous sections and in Chapters 4 and 6, transects and camera trap locations were randomly located based on a stratified-random design independent of any known bear distributions. Observations of Ursidae foraging behaviour suggest bear movement patterns are at least semi-random (Jonkel and Cowan1970, Rogers 1976, 1977, Jonkel 1984, Augeri 1994, Craighead *et al.* 1995, Mace and Waller 1997, Powell *et al.* 1997) and mean published sun bear home ranges on Borneo are between $4 - 14.8 \text{ km}^2$ (Meijaard *et al.* 2005). Although transects were independent and random, the individual sections on each transect were not; rather they were located systematically in successive line along the transect. Nevertheless, the likelihood that a bear crosses a particular point along a randomly placed 1,000 x 10 m strip (or a 2 - 3 m long

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infra-red camera-trapping beam) within its multi-square kilometre range, and leaves sufficiently conspicuous signs to be observed at a particular point in time at those specific locations, has a high probability of being a chance or random event. Thus, transects and their individual 100 m sections were considered independent for these analyses.

Finally, a potential problem is that species may be undetected, even though they are present. Potential violation of this assumption was minimised by the randomised- and nested-study designs and sampling theory. First, random-sampling theory supposes that not all objects or animals need to be sampled to generate a population estimate or other statistic of the population (Ott 1988, Ott and Longnecker 2001, Fowler *et al.* 2001). This study design, the Distance-sampling method and model, and the MacKenzie *et al.* (2002) model are all based on random-sampling theory and, thus, non-detections were accounted. With a randomised-sampling design of multiple independent samples, absence is accommodated in the MacKenzie *et al.* (2002) and Distance models by estimating probabilities of detection and non-detection. A nested-experimental design of random independent surveys in multiple habitats at multiple sites reduced independence violations and enabled more accurate detection probabilities. Thus, robust estimates were possible of detection-non-detection and consistently occupied sites (MacKenzie *et al.* 2002, 2003, Royle and Nichols 2003).

5.4 Scat Sampling

Bear scat samples were collected *via* habitat and sign surveys as well as opportunistically. Scat samples were collected in plastic bags, were later dried in trays and on newspaper in the sun, and the contents were separated and examined. While some plant matter and seeds are not altered to any notable degree when passing through a bear's digestive system, animal flesh in scat is substantially reduced (Hatler 1972). Scat analyses by Fredriksson (1998) of habituated free-ranging and wild sun bears in Sungai Wain Protection Forest indicated that sun bears may concentrate on fruit, plant, and insect biomass, much of which is sustained through the digestive process. Wong (2002) observed similar feeding behaviour in Sabah and this was the case with the majority of scat samples from my studies in East Kalimantan, Aceh, and North Sumatra.

Once scat samples were dried, the contents were sifted, separated, and grouped according to type. In the frequent case of insect parts, particularly termites, pieces were sorted by using a hand lens. Occasionally scats composed of bee hive remains were found, containing no other items. Other items, such as bear hairs in the scat were collected with sterilised tweezers and stored for genetic analysis in clean envelopes made by a female

assistant to avoid chromosome contamination from male handling. Envelopes with hairs were then stored inside plastic bags with indicating silica beads.

Correlations among diet and habitat use were examined using logistic regression analyses and differences were tested by Chi-square (X^2) tests and General Linear Models (GLM) as outlined in section 5.7. Analyses were focussed on patterns of sun bear resource use relative to biogeographic, general habitat, disturbance, and interactive variables.

5.4a Assumptions

Only data from feeding sites assumed with high confidence to be from a sun bear were recorded, but without actual observation of the bears eating, bear signs are only indirect evidence of the their feeding behaviour. It is certain that other mammals like pangolin (*Manis javanica*), pigs (*Sus spp.*), civets (Viveridae spp.), Malay badger (*Mydaus javanensis*), porcupine (*Hystrix spp.*) and other species create similar feeding evidence. To improve the probability for the assumption that feeding signs were made by sun bears, we recorded only data from scats most certain to be from bears, based on all known indicators of bear scat size, shape, contents and associated signs, such as tracks and markings most probably associated with the scat deposit, and only from feeding sites where bear claw marks, tracks, or other definite sun bear signs were observed. We also collected uneaten food items from verified sites for identification and comparisons with samples from other sites.

5.5 Fruit and Tree Stand Productivity

The hypothesis that sun bears provide community level services, such as facilitating seed dispersal and establishment, was examined by testing significant differences in sun bear resource use among sites in different biogeographic and disturbance conditions. McConkey and Galetti (1999) suggested that sun bears may provide important seed-dispersing functions for many plant species in Kalimantan. Unfortunately, seeds, nuts, and other foods are not equally distributed within any particular scat sample. Thus, fruit productivity, forage diversity, and habitat character were assessed on the same transects as sign censuses to test correlations between bear habitat selection/use and potential habitat or disturbance effects.

Each 1,000 m sign census transect was measured with a hip-chain to 0.1 m accuracy and was subdivided into 100 m units, which were marked and numbered with flagging ribbon. A 20% stratified-random sample (2 x 100 m units) on each transect was then surveyed for fruit productivity, forage diversity, and tree stand character. Protocol followed randomisation theory as described by Ott (1988), which suggests a minimum sample size (n) of n = 25 - 30 sample sections for each survey site. This produced a total of 64.2 ha of sampled area, of which 59.4 ha were used for the current analyses. A range of 1.2 - 9.6 ha was sampled for each habitat or disturbance type, depending on total survey area available.

All trees ≥ 10 cm dbh within the 100 x 10 m survey sections were measured and their perpendicular distance to the centre line was recorded. Survey sections on each transect were selected using a stratified-random design according to the following criteria:

- (1) Sections with the least amount of signs were compared against sections with the highest sign frequencies, but both sections had similar biogeographic characteristics.
- (2) Sections with similar sign frequencies, but different biogeographic characteristics were compared.
- (3) Undisturbed sections were compared against disturbed sections with similar biogeographic characteristics.
- (4) All else being equal, two completely random sections were compared.

Site and habitat assessment parameters are listed in table 5.3. All trees ≥ 10 cm dbh were identified for species and physical characteristics, such as height, dbh, maturity level, emergence, crown status, and canopy cover. Diameter at Breast Height (dbh) was calculated by recording tree circumference at breast height in the field, which was later converted to dbh for each tree based on the common equation from Euclidean geometry:

$$diameter = \frac{circumference}{\pi}$$

Basal area (G/m^2) was derived for each tree from dbh using the standard silviculture equation:

$$G = (dbh)^2 \times (0.0000785398)$$

Fruit and flower productivity scoring (*ps*) for each censussed tree was conducted on a five-point ordinal scale of 0 - 4, where 0 equals no fruiting (0%) and 1,2,3,4 equal approximately: 1 = 1 - 25%, 2 = 26 - 50%, 3 = 56 - 75%, and 4 = 76 - 100% of the degree of fruiting on the particular tree or plant. This is a relative measure and it is recognised the scale is semi-quantitative, but it has been tested and successfully used with similar studies in the Tropics (Renvoize 1975, Hill and Newberry 1980, Peres 1991, Augeri and Pierce 1995). To improve objective estimates, a Densitometer (GRS 2001) graduated in 25% sections was used to quantitatify fruit or flower coverage. A Relative Productivity Index (PI) was developed and calculated for each section using the respective sums of the fruit and flower productivity scores in the formula:

$$PI = \frac{\sqrt{\sum ps(fruit) + \ln(\sum ps(flower))}}{Tn}$$

where *ps* is the productivity score for each tree in the 100 x 10 m section, ln is the natural log, and *Tn* is the number of trees surveyed \geq 10cm dbh in the section. This measure generated a relative productivity index (PI) of fruit and flowers for each 100 m section ranging between 0 – 1, where indices closer to 1 indicated higher productivity.

Given the high degree of variance between sites, all tree-stand data, including productivity indices, were transformed using square-root or log-based transformations in SAS (SAS 2002). Differences in bear sign frequencies relative to fruit productivity and other tree stand characteristics were examined by General Linear Model (GLM) analyses, as described in the statistical scheme discussed in section 5.7.

5.6 Habitat Surveys

Habitat data were used to analyse potential biogeographic effects on the spatial variation in bear resource and habitat use. Data were recorded in every 10×10 m segment along each transect as measured by a hip-chain with accuracy to 0.1 m. Biogeographic data collected for each segment along the entire length of the 1,000 x 10 m transects are noted in table 5.3. Each of these variables is described below.

Table 5.3. Biogeographic data recorded for each 10 x 10 m sub-section of every transect. These data categories were tested and validated during field trials in 1998, 2000, and 2001 and were used on all subsequent transects through the end of the study.

Canopy Cover (%)	Habitat Type and Characteristics
Ground Cover (%)	Forage Cover $(0-4)$
Slope (degrees)	Basic Available Forage (0,1)
Aspect	* Fruit
Elevation (m)	* Termite Colonies, Ant Colonies, & Other Insects
Distance to Water Source (m)	* Bee Hives
Predator Presence (0,1)	* Tubers, Mushrooms, Plants
Competitor Presence $(0,1)$	* Other Forage, including small vertebrates
Other Species of Concern $(0,1)$	Habitat Disturbance $(0-4)$ + (Type, Age, Distance, Extent)
Refugia (escape cover) $(0-4)$	Human Activity $(0-3) + (Type, Age, Distance)$

Biogeographic Data Recorded for Each 10m x 10m Segment on All Transects

5.6a Habitat type

The main habitat type (e.g. primary lowland forest, swamp, montane forest, heath forest, etc.) and general characteristics (e.g. riparian, ravine, rocky, forest gap, etc.) were recorded for every 10 x 10 m sub-section.

5.6b <u>Topography</u>

Slope, aspect, and elevation. Slope was recorded using the angle meter provided on compasses. Aspect was recorded using the cardinal direction indicated by compasses. Elevation was recorded using digital altimeters and GPS to verify where possible.

5.6c <u>Water</u>

Water is important for all species and, thus, the position, distance to, and availability of water sources were recorded.

5.6d Cover

Canopy cover (%) was estimated using a densitometer (GRS 2001) that was graduated into four equal sections representing 25, 50, 75, and 100% canopy cover of the 10 x 10 m transect sub-section. The same protocols used in preliminary surveys were employed here. According to Graphic Resource Solutions (2001), a cover estimate with this densitometer based on a sample of 100 points yields a 95% confidence interval between \pm 6.0 – 10.1% cover. An estimate based on 200 points produces a 95% confidence interval of \pm 4.3 – 7.1% cover. At least 1 reading/10m sub-section was taken on each transect, producing a minimum of 100 readings/transect.

Preliminary study results in 2001 showed that the average stand density of trees ≥ 10 cm dbh was ca. 4.84 trees/10 x 10 m sub-section. For 100% canopy cover in that 100 m² area, the average crown was estimated at 20.68 m² with a diameter of 5.13 m. This calculation was based on: area = Πr^2 . This crown diameter is within the range reported by Richards (1998) for Dipterocarpaceae in Sarawak and accounts for variance where some crowns will be ≥ 5.13 m \le and range to more than 10 m diameter depending on the species, tree maturity level, site, and conditions. Thus, in cases where densitometer results were inconclusive or difficult to acquire, canopy cover estimates were cross-referenced by using a scale based on 4.84 trees ≥ 10 cm dbh/100 m² (10 x 10 m) sub-section (table 5.4).

Number of Trees	% Geographic Coverage	Score
0	0%	0
1 - 1.2	1-25%	1
1.3 - 2.4	26 - 50%	2
2.4 - 3.5	51 - 75%	3
> 3.6	76 - 100%	4

Table 5.4. Average canopy cover based on 4.84 trees ≥ 10 cm dbh per 100 m² sub-section.

Ground cover (%) was defined as the horizontal coverage of shrub, plant, seedling, and sapling growth < 1.5 m tall. Coverage was estimated by inverting the densitometer graduated in 25% sections at a 90⁰ angle and estimating the horizontal foliage and stem cover across the 10 x 10 m sub-section.

Escape cover ("Refugia") (%) was defined using the availability of mature trees ≥ 20 cm dbh along with canopy cover, ground cover, rocky out-crops, riparian zones, gullies, and steep ridges for escape. Escape cover was calibrated on a 5-point ordinal scale of 0 - 4 of the percent geographic coverage in 25% increments in the 10 x 10 m sub-section, such that zero = no cover (e.g. clear-cut with all biomass removed) and ranging to 4 = a minimum of 2 - 3 mature trees in $\ge 90\%$ canopy cover and > 15 - 20% ground cover.

5.6e Primary Forage Abundance

Forage (e.g. fruit, termites colonies, bee hives, etc.) abundance was estimated by counting 1 for the presence of each separate known bear food type in the 10 x 10 m subsection. Food items that were part of the same source, such as all of the fruit from one tree or an entire termite colony, would be considered one item. Totals for each food type were then summed at the end of each 100 m section. A constant of 2 unknown items was added to all 100 m sections, because it is certain some bear foods were either not observable or were missed, e.g. sub-terrainean termite colonies.

5.6f Primary Forage Cover (%)

Scores of percent cover of bear foods were measured according to the sum total geographic coverage of all foods in the 10 x 10 m section. Scores were based on a 5-point ordinal scale: 0 = 0%, 1 = 1 - 25%, 2 = 26 - 50%, 3 = 56 - 75%, and 4 = 76 - 100% cover. Estimates of geographic coverage used the criteria listed in table 5.5, which were based on

the average observed geographic extent of these particular food items during preliminary surveys as measured by tape measure and/or GPS.

Fruit cover varied and was a special consideration. Fruit cover for each 10 x 10 m sub-section was based on the same 5-point ordinal scale (0 - 4) representing 0 - 100% of the degree of fruiting on the particular tree or plant. A Densitometer (GRS 2001) graduated in 25% sections was used to estimate total fruit coverage of the 10 x 10 m sub-section. Preliminary research in 2001 showed that the average fruit coverage was 32% across all surveyed sections (Augeri, unpub. data).

Table 5.5. Criteria delineating primary forage cover in 10 x 10 m transect sub-sections. Note that these covers are based on average geographic extent and some items vary in size, e.g. some below ground termite colonies are $> 5 \times 5 m$, whereas some are $< 5 \times 5 m$ (Fredriksson pers. comm.)

Food Item	Geographic Cover	Scale (% of 10m x 10m	Score	
	Cover	0 fruit	- 0	0
	Variable (based	1 25	-1.25	0
Fruit	on densitometer	1-23	-1-23	2
TTutt	on densitonieter	20-30	-20-30	2
	estimates)	51-75	= 31 - 75	3
		/6-100	= /6-100	4
Termite and		0 colonies	= 0	0
Ant		1-6 colonies	= 1-25	1
Colonies	4 m^2	7-12 colonies	= 26-50	2
(above	1 111	13-20 colonies	= 51-75	3
ground)		21-26+ colonies	= 76-100	4
	25 m ²	0 colonies	= 0	0
Termite		1 colony	= 1-25	1
Colonies		2 colonies	= 26-50	2
(below ground)		3 colonies	= 51-75	3
ground)		> 4 colonies	= 76-100	4
Bee Hives	4 m ²	0 nests	= 0	0
		1-6 nests	= 1-25	1
		7-12 nests	= 26-50	2
		13-20 nests	= 51-75	3
		21-26+ nests	= 76-100	4
Other		0 items	= 0	0
Forage	Forage (tubers, 1 m ² other insects, etc.)	1-25 items	= 1-25	1
(tubers,		26-50 items	= 26-50	2
other		51-75 items	= 51-75	3
insects, etc.)		76-100+ items	= 76-100	4

5.6g Forage Relative Abundance Index

A forage richness and diversity index was developed to address the assumption that different habitats and disturbed areas provide varying diversities and availabilities of bear forage. Primary sun bear foods (fruit, termite colonies, bee hives, etc.) have patchy distributions in both time and space, where the absence of some preferred items is compensated by the presence of secondary items during opportunistic foraging bouts. This index was developed to measure the proportional representation of each food item by abundance, variety, and geographic extent, such that forage richness and the proportional diversity of all available foods at the time of surveying were combined in one index. This forage Relative Abundance Index (RAI) was calculated by:



Because some foods are prevalent but not as important in the bear's diet, this is a proportional diversity measure of the relative abundance, variety, and cover of available foods. The sum of each available food item f as represented by i (e.g. fruit, termite colonies, bee hives, etc.) is proportional to the total available forage (T) in the larger 10 m x 100 m section, where T is based on the sum total occurrence of all food items present in that 10 m x 100 m section. If an item is available, it is scored as 1. If an item is present, but not available for forage, such as a *Ficus* spp. source that is not producing, then it was still ranked as 1 because it could be available at some other time. It is certain that the estimated or observed number of bear food items surveyed was lower than actually exist (i.e. subterranean termite colonies, other insects, bee hives, etc.) and the total is squared.

This proportional representation of available foods is relative to their individual geographic extent or coverage C_i according to one of the 5 cover classes described above (0 = 0%, 1 = 1 - 25%, 2 = 26 - 50%, 3 = 56 - 75%, 4 = 76 - 100%). This proportion must be considered relative to the diversity or variety v_i of available foods and their geographic cover, which are then used as multiplicative factors in the equation. This measure generated a relative abundance index (RAI) ranging between 0 – 1, where scores closer to 1 indicated higher diversity. Given the variance between sites and transects, the index results were square-root transformed in SAS.

5.6h Competitive and Agonistic Relationships

Interactions and use of habitat by potential sympatric competitors and antagonistic species can influence bear movements, habitat use, range, behaviour, health, survival and fitness. As with other Ursidae, an important influence on sun bears is often competition for food and space. In addition to niche expansion to take advantage of arboreal fruit sources, the evolution of sun bear arboreal behaviour and general range and landscape use has also been potentially influenced by the co-evolutionary forces of predation and antagonistic
interactions. Thus, the effects of competition and predation at 0.1 m resolution every 10 m were recorded based on absence (0) or presence (1) (based on sightings, calls, tracks, claw marks, scat, etc.) of sympatric competitors and antagonistic species like tigers and leopards.

5.6i Human presence

Human activities can influence animal movements and behaviour, including bears (Mattson *et al.* 1987, Mattson and Knight 1991, Craighead *et al.* 1995, Powell *et al.* 1997, Bader 2000, Morrow 2001, Craighead *et al.* 2001, Maher *et al.* 2003, Larkin *et al.* 2004). This effect was measured by a 4-point ordinal scale of 0 - 3, where 0 = no human presence, $1 \le 25$ people present/week, 2 = 25 - 50 people present/week, and 3 = 50+ people present/week. The type of activity (e.g. hunting, gathering, farming, trail use, river traffic, etc.), age, and distance to these activities were recorded. Distances were measured with GPS or tape measure. Measurement of the number of people and type of activities in specific areas was based on **(a)** direct observations during field surveys, **(b)** counting and interviewing hunter/gatherers obligated to pass through the research station to and from their forays, and **(c)** informed knowledge from the project's chief local assistants, including the Kapala Adat (traditional leader), who worked as the project's lead field assistant in East Kalimantan, and who knew and endorsed local users along with when and where they were in specific hunting/gathering grounds, their activities, and their quarry.

5.6j Hunting Surveys

Social surveys regarding hunting activities were conducted in local villages in all major study areas. Methods followed Fishbein and Ajzen (1975) and a standardised approach and questions were used. Local field assistants were first selected randomly in each site and open-ended questions regarding wildlife, forest ecology, and hunting were posed to generate standardised questions with a 5-point Likert scale for responses for the main survey (Fishbein and Ajzen 1975, Ajzen and Fishbein 1977). General questions were designed to gauge general knowledge of sun bears, wildlife, and forest ecology. The main questions were designed to examine local and annual trends in hunter take of sun bears within and between areas. ANOVA and Kruskall-Wallis tests were used to examine differences. Due to the nature of local cultural values, especially toward foreigners in remote areas, written questionnaires were not accepted in all cases. Thus, verbal methods were adopted. Village leaders were surveyed systematically while the general public were surveyed randomly using standard protocols. The standarised scientific questionnaire with the 5-point Likert scale was used in all cases, but questionnaires were posed verbally for standardization across sites.

5.6k Habitat Disturbance

The types, ages, intensities, and geographic extent of habitat disturbance can influence animal movements, behaviour and ecology, including for bears (Mattson *et al.* 1987, Servheen *et al.* 1999, Bader 2000, Morrow 2001, Craighead *et al.* 2001, Maher *et al.* 2003, Larkin *et al.* 2004). Habitat disturbance types were logging, agriculture, roads, edges, villages, burned areas, large high-traffic human trails, etc. Intensity was based on a 5-point ordinal scale of 0 - 4, where 0 = no disturbance and 1 - 4 represent 1 - 25%, 26 - 50%, 51 - 75%, or 76 - 100% respectively, of the amount of the original area disturbed. For example, one tree cut for gaharu in which > 95% of the original habitat remaining in the surveyed area was scored as level 4. Less than 50% of the original forest remaining was level 3, between 50 - 75% remaining was level 2, and more than 75% remaining was level 1.

Extent was based on the actual geographic coverage (m^2) of disturbed area and was measured using GPS coordinates, maps, GIS, or tape measure. Some undocumented cases, such as new multi-hectare or larger disturbed areas, required estimation. Disturbance types included logging, agriculture, trails, roads, villages, and so forth and their after-effects like secondary growth in variously aged stands. Ages were calculated on a monthly scale, such that 1 day old = 0.03 months, one week = 0.23 months, one year = 12 months, and so forth. Distances were measured with GPS or tape measure.

5.61 Limitations

General limitations and assumptions for habitat assessments, such as habitat differences, logistical constraints and so forth, are listed in Section 4.6 and are addressed in specific method sections in Chapter 5 where applicable. The most obvious limitation for habitat assessments is that some of the variables were generated on a semi-quantitative basis. This limitation was minimised by (1) quantifying the particular variable as much as possible in a multi-variable mixed-sampling design, (2) extensive testing and field trials of both the methods and observer reliability prior to and during the full-time study, and (3) applying randomisation and sampling theories for methods/designs of surveys, accounting for and minimising observer bias as well as missed observations (Buckland *et al.* 2001).

5.7 Statistical Tests

The sampling design and two-stage nested experimental design described here and in Chapter 4 enabled tests of whether particular biogeographic conditions or disturbances statistically affected bear resource selection, movements, habitat use, and so forth. This was accomplished by testing the differences between variables (e.g. bear sign frequency) in treatments of disturbed habitat *versus* control sites of undisturbed habitats in primary forest. This was done relative to disturbance type (clear-cut, selectively logged, plantation, fire, etc.), habitat type, and other biogeographic variables like topography, forage abundance and diversity, presence of competitors or antagonistic species, and so forth. All tests were conducted across time and seasons to account for temporal variability.

Raw data were tested for normality, kurtosis, and skewness by descriptive measures in SYSTAT version 10 (SPSS 2000) or SAS version 9.1 for Windows (SAS Institute 2002). Each variable was also tested for homogeneity of error variance and normality was examined using probability plots of residual *versus* predicted values in SAS (Ott 1988, SAS Institute 2002). Square-root or various log-based transformations were sufficient for skewed data.

Data were first analysed at the observation level, e.g. 10 m and 100 m survey sections along transects. Perhaps the most important assumption of such field research is independence among variables and surveys. In terms of surveys, independence was improved by the randomised study design for both sign surveys and camera-trapping (Chapter 6), as described in their respective sections, and by the two-stage nested experimental design (Chapter 4), which grouped focal variables according to their common transect, habitat type, and so forth. Grouping increased test power by decreasing (1) violations of independence, (2) assumptions of inter-dependence among variables, (3) variance and systematic error within and between surveys, (4) variance and bias between surveys and treatments, and (5) variance or bias between observers.

Although independence issues arise at the 10 m level, this scale is ecologically important for sun bears, particularly regarding the availability of food items in their spatially and temporally patchy environment. Thus, several statistical schemes were used at the observation level, 10, 100, 200 m scales, and the nested-group level to test the significance of various biogeographic and anthropogenic effects on sun bear resource selection and habitat use. Observational and transect-level analyses are provided in the results. All tests were conducted in SAS version 9.1 for Windows (SAS Institute 2002) or SYSTAT version 10 (SPSS 2000) as described below:

- (1) ANOVA and non-parametric analyses (e.g. Kruskal-Wallis and Mann-Whitney U) were used to test differences in sign abundance among transects and treatments in different habitat types, disturbances, study sites, and so forth.
- (2) General Linear Models were used to test differences among bear sign frequencies in different habitats as affected by biogeographic and disturbance variation. These models were particularly useful for testing interaction effects among influential

variables on bear sign frequency, such as the extent, age and distance of habitat disturbance relative to where and when bears were active.

- (3) Linear and logistic regression analyses were used to test the relationship between the proportion of bear habitat use relative to independent variables, such as biogeography, topography, and disturbance.
- (4) Other tests, such as Pearson and Spearman's rank correlations, Chi-square, positive matching dichotomy correlations (S²), and Odds Ratios were used to examine any potential associations between, for example, sign abundance in a particular habitat type and its associated forage diversity, competitive overlap, and so on.

Descriptive measures, frequency analyses and statistical tests were performed on both individual and grouped variables. Model error variance (H_oe) for normal data was first tested using an ANOVA one-way or two-way experimental design. Chi-square (X^2) tests and logistic regressions were used for pair-wise comparisons of categorical variables within and between treatments to test significant differences between, for example, sign types relative to specific habitat types, disturbances, and their uses by bears. For consistency, ANOVA and non-parametric one-way tests using Kruskal-Wallis analyses of model significance and significant differences within and between treatments were used to test continuous variable responses, such as bear sign abundances in different habitats and disturbances. General Linear Models (GLM) of grouped sampling units and ungrouped observations were used to test for treatment and interaction effects, such as the extent, age and distance of habitat disturbance, biogeographic variation, human presence, and so forth, relative to where and when bears were active. Random (e.g. transects) and fixed-effects (e.g. habitat types) were examined in Mixed Regression and ANOVA models.

For example, individual and grouped variables were quantified by their median error variances (Inter-Quartile Range (IQR)) and differences were tested both within and between treatments. Here, the IQR error variance of a particular parameter (e.g. amount of sign/unit area) within a treatment (e.g. undisturbed lowland forest) was first determined for each test group (e.g. number of sign samples averaged across survey units) using SAS. Variability within a treatment was determined by testing that parameter's variance for significant differences among all test groups within that treatment using tests such as ANOVA and Kruskal-Wallis. This IQR error variance was then tested for significant differences with other treatments (e.g. amount of sign/unit area in a selectively-logged lowland forest site, swamps, secondary forests, etc.) through General Linear Model procedures. This procedure was repeated for all potential parameter effects, including interactions among independent variables on bear sign abundance and locations.

Correlation analyses were used for fruit productivity, forage diversity or habitat character relative to sun bear sign abundances in, for example, disturbed *versus* undisturbed habitats. In some cases, topography may cause differences in habitat character as well as bear responses to disturbance in the landscape (Augeri 1995). Thus, linear regressions were performed for continuous variable (e.g. slope, elevation) relationships with bear habitat use. Logistic regression and Kruskal-Wallis (X^2) tests were used for differences between, for example, sign abundance and topographic aspect in various habitats. Frequency distributions and descriptive statistical measures were calculated for most variables, such as canopy cover, mean dbh of bear sign trees/site, and so forth.

5.8 Diversity Models

Diversity calculations were conducted for general tree species diversity, bear tree species diversity (i.e. trees selected by bears), competitor species diversity, bear size/age class diversity, and general vertebrate diversity observed through sign surveys and camera trapping (Chapter 6). All diversity measures were performed in PISCES Species Diversity and Richness III software, version 3.03 (Pisces 2002). The five most robust diversity indices (Pisces 2002) were used for all diversity tests. These indices were the Shannon-Wiener H, Simpson's D, Margalef D, Berger-Parkar Dominance, and Fisher's Alpha, along with the Rényi Diversity Ordering Index. Details of each index are described in program PISCES. The purpose for each index used in this study were as follows:

- (1) Shannon-Wiener *H* was used to measure the proportion of individuals in the *i*th species or group. This index was useful as a general measure of diversity relative to abundance.
- (2) Simpson's *D* was used to examine the probability that a second individual drawn from the population is from the same group or species as the first individual and so on. The statistic provides a measure of the probability of the next encounter being different. This index is strongly influenced by the number of observations (generally > 10) underlying the distribution (Pisces 2002).
- (3) Margalef *D* was used to calculate the group or species number relative to the total number of individuals. This index was useful for its simplicity and proportionality relative to the total population.
- (4) Berger-Parker Dominance was used to examine heterogeneity of sites based on the numerical importance of the most abundant species or group. The reciprocal of the index, 1/d, was used so that an increase in the value of the index corresponds with an increase in diversity and a reduction in dominance.

(5) Rényi Diversity Ordering was used because different diversity indices differ in how they rank diversity among sites. The Rényi Diversity Ordering measure was used to identifying those sites that were most consistent in their relative diversity.

Differences in diversity measures between the various treatments were tested using a "bootstrap" randomization test for significant difference between two samples (Solow 1993). Bootstrapping enabled inferences about differences between populations from the data contained in a sample that was drawn from those populations. In this case, thousands of hypothetical or "bootstrapped" samples were created in programme PISCES for each diversity index, which was calculated for each hypothetical sample by randomly selecting values from the original sample. Programme PISCES conducted this test by re-sampling or "bootstrapping" 10,000 times from a distribution of species abundances produced by a summation of the two samples (Pisces 2002). This re-sampling was under the assumption of no change, such that the probability p of partitions of the combined data sets $m_1 + m_2$ is equally likely (Solow 1993). The test was conducted under the null hypothesis that there were no differences or changes in diversity between samples, where:

$$p = \begin{pmatrix} m_1 + m_2 \\ m_1 \end{pmatrix}^{-1}$$

Inferences of statistical differences were then made based on the differences in the distributions of thousands of bootstrapped samples of the test statistic between two populations. This procedure was repeated for each treatment pair, e.g. bear tree diversity in primary forest *versus* 20 year old secondary forest, and so on.

5.8a Assumptions

Each of these models has inherent assumptions. In general, some degree of statistical inference is necessary for these types of studies. The most common assumption was that each model has some basis in sampling and probability theories, such that diversity was measured from a sample of the population and the models then predicted final estimates as appropriate representations of the overall population. Application of the theoretical foundations of sampling, randomisation, and probability theories helped minimise this limitation. These theories are well tested in the literature (Ott 1988, Ott and Longnecker 2001) and were applied to this study, as described where applicable.

RESULTS

5.9 Sign Census Effort

Over a 28-month survey period between 2000 – 2003 a total of 335 km of transects and 64.2 ha of tree stand and fruit surveys were conducted across the 16 study sites as well as an additional ca. 1,200 km of pre- and post-transect surveying. An average of 10 hours were required to complete one transect and stand survey by three workers producing a total effort of 9,882 hours of actual survey time. Pre- and post-transect surveying added an average of 4 hours/transect amounting to an additional 4,020 hours. Hence, total census effort was 13,902 survey hours.

Preliminary censuses in Aras Napal and Kayan Mantarang during 10 February – 18 March 2000 (n = 14) and in Ketambe (n = 24) during 3 September – 4 November 2001 are not included in the present analyses. War in Aceh prohibited continuing study at Ketambe. All of these preliminary censuses functioned as test studies to (a) examine sun bear behaviour and habitat use and (b) test and refine methods, sign aging, habitat bias, and so on. Thus, 297 transects between 12 November 2001 - 10 July 2003 were used for the present analyses. A total of 4,886 distinct sun bear sign observations were recorded in all habitat types on 297 transects, of which no signs were recorded on 47 kilometres. The locations, census areas, and frequencies of sun bear sign events by general habitat types for the present analyses are summarised in table 5.6.

5.10 Bear Sign Types

A wide variety of bear sign types (n=27) were observed (table 5.7), of which the significant majority (96.2%) were related to trees (X^2 = 74250.7, P < 0.0001). Sign evidence indicated that the majority of trees (76.6 %) were likely climbed for fruit consumption, followed by climbing for bee hives (9.3%), climbing for unknown reasons (7.7%), and climbing for insect foraging (1.6%), of which ca. 86% were specifically for termite foraging. One other dominant tree use (n = 40) appeared to be non-climbing territorial or range marking behaviour at the base or lower trunk of trees, which is typical of other Ursidae. The latter use was a small amount of observed signs (0.82%) compared to other sign types.

The most dominant non-tree signs were termite diggings, but again relative to bear use of trees this was minor at only 1.7% of all signs observed. A small number of diggings were observed at the base of trees for bee hives as well as a few ground diggings for unknown reasons (possibly exploratory for termites). At least 14 tree nests were recorded

Region	Focal Area	Site	General Habitat Type	Number of Transects (km)	Stand Surveys (ha)	Total Sign	Sign Frequency/ha	% Pre Disturbance
Sumatra	Gunung Leuser	Sekundur	Secondary Forest (lowland) (1 - 23 yrs old)	16	3.2	95	5.94	89.5
	East Plain	Gunung Runtuh	Secondary Forest (lowland) (1 - 20 yrs old)	24	4.8	228	9.50	100
	Comment I and an	Sei Badak	Primary Forest (low/mid-elev)	40	8.0	572	14.30	100
	East Slope	Tankahan	Primary Forest (montane)	24	4.8	326	13.58	100
	Leuser East Plain	Aras Napal	Agriculture and Edge (lowland)	48	9.6	180	3.75	99.5
		Lalut Birai	Primary Forest (low/mid-elev)	19	3.8	601	31.63	100
	Kayan Mentarang National Park	Jalungkereng	Primary Forest (low/mid-elev)	8	1.6	275	34.37	100
		National Park Nnggeng Tau Pr		Primary Forest (mid-elev)	9	1.8	299	33.22
		Ulu Stee	Primary Forest (mid/elev montane)	18	3.6	829	46.05	100
		Bahau Primary Forest	Primary Forest (lowland)	12	2.2	260	21.66	100
Borneo	West Bulungan	Bahau Secondary Forest	Secondary Forest (lowland) (1 - 25+ yrs old)	11	2.0	120	10.91	100
		Alango	Agriculture and Edge (lowland)	8	1.6	16	2.00	100
		Seturan	RIL/CNV Logging Primary Forest (lowland)	24	4.8	293	12.21	98.3
	East Bulungan	Gunung Sidi / Loreh	RIL/CNV Logging Primary Forest (lowland)	6	1.2	100	16.66	98.0
		South Seturan	Primary Forest (lowland)	19	3.8	462	24.30	100
		Tukuk Mawot	Primary Forest (mid-elev)	11	2.2	230	20.91	100
			TOTALS	297	59	4886		

Table 5.6. General Summary of data used in current analyses. Note: % pre-disturbance is < 100 m from moderate to high disturbance.

and confirmed as used or explored by bears. In these cases, confirmation was possible because the nests were (a) in areas with known orang-utan absence and/or (b) confirmed with bear hair and claw marks from ground to nest. At least 49 independent track set events were also recorded. Track sets were counted as separate sign events from each other only when they were (a) different ages, (b) obviously different size classes (i.e. cub *vs.* adult), or (c) more than 100 m apart. The vast majority of track observations were isolated events of only one observation/transect. Track observations of more than one event/transect were rare, occurring in only 8% of the total track observations. Thus, minimal track crossings were observed on any one transect.

Table 5.7. General summary of observed independent bear sign events. A total of 27 different signs were recorded. Note that "tree tear" sign included climbing the tree to access the noted type of foraging, such as for bee hives, termites, etc. Additional hair and scat samples (+) were found during pre- and post- transect surveys and are not included in the total independent sign events observed for transect censuses.

Bear Sign Type	Frequency
Claw Marks (climbed for fruit)	3,744
Claw Marks (undetermined use)	378
Tree Tear (bee hive foraging – stingless bees)	377
Sub-terrainian Termite Excavation	82
Tree Tear (bee hive foraging – general)	77
Tree Tear (termite foraging)	68
Tracks	49
Claw Marks (territorial - non-climb)	40
Nests	14
Log Tear (insect foraging)	13
Scat	10 (+ 30)
Claw Marks (no climb)	8
Earth Dig	8
Tree Tear (insect foraging – general)	8
Bear Hair	1 (+ 7)
Bee Hive Dig	4
Tree Tear (ant foraging)	2
Bee Hive Remains	1
Den (hollowed log)	1
Sightings	1
Total Independent Sign Events	4,886

When comparing general characteristics of bear signs across focal areas and regions the same general patterns emerged, despite significant geographic separation among study areas between Sumatra and Borneo (tables 5.8 and 5.9). Overall, observed signs were on average about 2 years old (range: 1 day - 10 years), were located in forested areas with a mean canopy cover of 95.8% (range: 0 - 100%) and 16.9% ground cover (range: 0 - 100%) on an average slope of 24.17 (range: $0 - 86^{\circ}$) at mean elevations of about 420 m asl (range: 29 – 1,292 m asl). Average sign site elevations were notably higher in East Kalimantan (474.43 m asl) than in North Sumatra (263.25 m asl). Sign tree dbh averaged 43.74 cm (range: 3.25 – 926.43 cm) and mean height was 18.37 m (range: 1-55 m). As discussed in proceeding sections, the diversity of tree species selected by sun bears was significantly higher in primary forests than in all other habitat types. Sign trees were marginally taller in Sumatra, but slightly wider in East Kalimantan. At the same general time when bears produced signs, disturbance and human activity levels were minimal to none, averaging 0 (range: 0-1) and 0.09 (range: 0-2) respectively. Although the parameter ranges reported here indicate minimum and maximum results, some of these are outliers and their means reflect more consistent characteristics of observed signs.

General Sign Traits	All Sites	East Kalimantan	North Sumatra
Age (months)	24.57	26.69	18.44
Sign Tree dbh (cm)	43.74	43.96	43.13
Sign Tree Height (m)	18.37	18.25	18.72
Canopy Cover (%)	95.79	96.35	94.19
Ground Cover (%)	16.92	17.82	14.33
Slope (degrees)	24.17	25.92	19.09
Elevation (m asl)	420.29	474.43	263.25
Disturbance Intensity (0-4)	0	0	0
Human Activity Level (0-3)	0.09	0.11	0.04

Table 5.8. Means of general characteristics of observed sun bear signs across all sites in the project and separately for North Sumatra and East Kalimantan.

Sun Bear Ecology, Habitat, and Landscape Use Results

Region	Area	General Sign Traits	Mean	Std Dev	Min	Max	Region	Area	General Sign Traits	Mean	Std Dev	Min	Max
		Age (months)	13.13	6.96	1.0	24.0		Kayan Mentarang National Park	Age (months)	20.13	24.95	0.03	132.0
	A 105	Sign Tree DBH (cm)	51.62	38.65	15.10	213.76			Sign Tree DBH (cm)	44.91	32.80	3.25	414.17
		Sign Tree Height (m)	18.63	6.39	3.0	36.0			Sign Tree Height (m)	18.14	6.03	3.0	45.0
		Canopy Cover (%)	83.55	22.88	10.0	100.0			Canopy Cover (%)	98.37	5.97	30.0	100.0
	Nonal	Ground Cover (%)	15.0	5.32	0	25.0			Ground Cover (%)	19.81	11.65	0	100.0
	тара	Slope (degrees)	14.90	7.85	0	32.0	East Kalimantan		Slope (degrees)	30.27	13.41	0	70.0
		Elevation (m asl)	61.39	21.18	29.0	112.0			Elevation (m asl)	573.72	103.40	315.0	988.0
		Disturbance Level (0-4)	0	0	0	0			Disturbance Level (0-4)	0	0.02	0	1.0
		Human Activity (0-3)	0.06	0.36	0	2.0			Human Activity (0-3)	0.15	0.36	0	1.0
	Gunung Leuser National Park East Plain	Age (months)	20.14	11.34	0.03	60.0		West Bulungan	Age (months)	20.29	27.36	0	120.0
		Sign Tree DBH (cm)	43.36	55.65	9.55	926.43			Sign Tree DBH (cm)	39.81	33.67	6.50	293.89
		Sign Tree Height (m)	17.97	5.40	1.0	35.0			Sign Tree Height (m)	19.14	7.71	1.0	55.0
Northorn		Canopy Cover (%)	92.38	12.63	25.0	100.0			Canopy Cover (%)	94.37	18.36	0	100.0
Sumatra		Ground Cover (%)	16.75	9.09	5.0	80.0			Ground Cover (%)	18.06	10.97	0	50.0
Sumatia		Slope (degrees)	10.77	12.67	0	46.0			Slope (degrees)	23.07	12.69	0	52.0
		Elevation (m asl)	74.84	17.48	35.0	151.0			Elevation (m asl)	453.46	86.75	59.0	706.0
		Disturbance Level (0-4)	0.02	0.14	0	1.0			Disturbance Level (0-4)	0.01	0.11	0	1.0
		Human Activity (0-3)	0.14	0.35	0	2.0			Human Activity (0-3)	0.14	0.35	0	1.0
		Age (months)	18.01	11.64	0.03	96.0			Age (months)	41.99	32.33	0.03	120.0
		Sign Tree DBH (cm)	42.76	24.60	6.56	268.95			Sign Tree DBH (cm)	44.24	35.73	6.05	416.37
	Gunung	Sign Tree Height (m)	18.99	6.01	2.0	50.0			Sign Tree Height (m)	18.03	4.68	4.0	40.0
	Leuser	Canopy Cover (%)	95.20	9.41	25.0	100.0	7	Fast	Canopy Cover (%)	93.61	12.22	20.0	100.0
	National	Ground Cover (%)	13.43	5.09	5.0	60.0		Bulungan	Ground Cover (%)	14.02	6.40	5.0	60.0
	Park	Slope (degrees)	22.23	11.99	0	86.0		Dulungan	Slope (degrees)	19.29	11.56	0	42.0
	East Slope	Elevation (m asl)	337.99	293.54	55.0	1292.0			Elevation (m asl)	301.39	176.88	56.0	830.0
		Disturbance Level (0-4)	0	0	0	0			Disturbance Level (0-4)	0	0	0	0
		Human Activity (0-3)	0.01	0.10	0	1.0			Human Activity (0-3)	0	0.05	0	1.0

Table 5.9. General characteristics of observed sun bear signs in the various study areas of northern Sumatra and East Kalimantan.

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Sightings: In almost 14,000 hours of surveying, only one wild sun bear was encountered. This event occurred at the completion of a transect at about 16:00 h in the upper Bahau river basin in the western region of the Bulungan ecosystem adjacent to Kayan Mentarang National Park. Our team of four men (3 researchers and 1 trainee) were in a primary forest area with 100% canopy cover and 10% ground cover 10 km from the nearest village. Three men were sitting while one man was standing taking a GPS reading and talking in a soft tone, when a medium-sized bear approached us to within 10 m. The bear approached us directly in a slow walk with its head down focused on and sniffing the ground. At about 10 m from our position the bear lifted its head, looked at us for about 3 - 4 seconds, turned and moved away at a 90-degree angle from our position. During the bear's departure, we were able to sex-type it as a male. The bear's movements could be characterised as a slow and unhurried walk when approaching us to within 10 m and a quick-paced trot when departing the area.

5.11 Sign Detection Probability

It is assumed that different habitat types will bias the probability that sign is detected (Garshelis 2000), where different tree species, substrates, bear sizes, and so forth will affect the detectability of various signs. Results showed, however, that ample sample sizes ($n \ge 20$ transects/habitat/site) of randomly-distributed independent surveys in multiple habitats across multiple sites minimised such biases. The primary assumption that surveys were random and independent was important for the accuracy of detection and occupancy probabilities. Model results in programme PRESENCE showed that as the scale increased from 10 to 500 m, the probability of sign detection, *p*, increased as expected, but the probability of occupancy, ψ , was unchanged across geographic resolutions. This suggests that regardless of scale, survey replicates at 100, 200 or 500 m were independent for these analyses.

At the macro-habitat scale, variance in the probability of detection, p, was lowest, and estimate precision increased, with increasing transect replicates in different habitat types. Multiple 100 m transect section replicates achieved the best model fit and increased the probability of detection at the micro-habitat scale. The probability of detection was higher at the 200 m section level than at 100 m, but habitat heterogeneity naturally increased as the survey area increased, which confounded estimate precision. Overall, micro-habitat estimate precision was best achieved *via* multiple replicates at the 100 m section level, where habitat character was more uniform and variance in the probability of detection was lowest.

Results of sign detection probabilities, *p*, in programme PRESENCE were not different among macro-habitat types and the asymptotic chi-square quadratic test (Sauer and Williams 1989) of these probabilities in programme CONTRAST (Hines 2004) did not reflect significant differences ($X^2=2.574$, df=6, P=0.8601). Detection probabilities *g*(0) using the best fitting models (Hazard-Rate Cosine and Half-Normal Simple Polynomial models) in programme DISTANCE (Thomas *et al.* 2003) showed a similar pattern ($X^2=11.878$, df=8, P=0.1567). For example, *g*(0) mean for primary lowland forests was 0.4795 (± 0.0578 SE) and the mean for secondary lowland forests was *g*(0) = 0.4621 (± 0.0693 SE). The detection probability in these undisturbed primary lowlands was slightly higher, but differences were not statistically significant with those in secondary forests ($X^2=6.873$, df=4, P=0.1427) or with other habitat types, such as primary mid-elevation forests, swamps, edges, ridges, and so forth ($X^2=23.225$ df=15, P=0.0795). In effect, overall general habitat biases did not significantly affect sign detection and, thus, comparisons among habitat types were possible.

Although there were no differences among habitat types, there were sizeable differences between undisturbed forests and various levels of disturbance (figure 5.4).

Habitat disturbance types varied and included logged forests, agricultural areas, roads, edges, villages, large high-traffic human trails, and so forth. The asymptotic chi-square quadratic test in programme CONTRAST resulted in significant differences in these probabilities among disturbed and undisturbed sites ($X^2=2367.42$, df=4, P<0.00001). These overall differences are not surprising considering that areas such as logged sites have, for example, fewer trees to detect claw marks and any existing signs in remaining trees or on the ground would be more exposed to weathering, resulting in lower detectability. Signs may be undetected even though they are present (MacKenzie *et al.* 2002), but model results showed that multiple surveys ≥ 20 in each habitat type increased the accuracy and precision of detection, decreased variance, and enabled occupancy estimates even when detection probabilities were < 1 in some cases (MacKenzie *et al.* 2002).



Figure 5.4. Detection probabilities from programme PRESENCE of various levels of disturbance *versus* undisturbed primary forests. Differences are significant (X^2 =2367.42, df=4, P<0.00001). PF=primary forest; SF=secondary forest.

Site occupancy is a direct function of detection probabilities and heterogeneity can, in some cases, reflect differences in either animal abundance or in basic detections (Buckland *et al.* 1993, 2001, MacKenzie *et al.* 2002, Royle and Nichols 2003). The large sample sizes across sites provided 95% confidence in detections, as seen in model results from both DISTANCE and PRESENCE. Model results indicated that heterogeneity existed in detection probabilities, but the most important source of such variance is likely animal abundance (Royle and Nichols 2003), in that p increases as the number of animals increases (Royle and Nichols 2003). Overall, the same pattern emerged across sites, focal areas, regions, and habitats of varying biogeographic and topographic characteristics: Sign detection and density probabilities were consistently higher in undisturbed sites.

5.12 Fixed-Width Transect Censuses

Given detection probability results, biogeographic parameters as well as disturbance and human activities measured along each transect could be tested for effects relative to habitat use by sun bears. Significant differences at the observation level (10 - 100 m) among all habitat types and disturbances demonstrated that sun bears were selecting primary undisturbed forests with minimal human activity significantly more than disturbed areas or young secondary forests (r²=0.685, F=1598.793, df =42, P<0.0001). Tests of transect means resulted in similar patterns (r²=0.655, F=24.10, df=21, P<0.0001). Logging, agriculture, and persistent human activity of non-timber forest-product harvesting, hunting, trail transit, and so on were the most statistically-significant factors associated with habitat avoidance by bears. Figure 5.5 illustrates these differences at macro-habitat levels across study sites.



Figure 5.5. Mean bear sign frequencies across all study sites at general macro-habitat levels. PF=primary forest, SF=secondary forest, RIL=Reduced Impact Logging and CNV= Conventional Logging.

East Kalimantan had the highest frequency of bear signs (n=3,634) and was 65.6% more abundant than in Sumatra (n=1,252). Kayan Mentarang National Park was most abundant (n=2,004), with 45.9% more signs than in the next highest focal area, the Bulungan Research Forest (n=1,085), and 72.8% more signs than in the Park's bordering unprotected area of West Bulungan (n=545). In Sumatra, the more remote undisturbed East Slopes of Sei Badak (n= 898) had 64.1% more signs than in its East Plain secondary forests (n=323).

The highest frequencies of bear signs were consistently observed in the least disturbed habitats surveyed. The undisturbed primary forests of the Jalungkereng area in Kayan Mentarang National Park, East Kalimantan had a high of 92 sign events/ha, but the more remote interior of the Ulu Stee of the Ulu Nnggeng region showed the most consistent and abundant bear signs of all sites, with a mean of 46.05 sign events/ha. Despite the fact that these areas are traditional hunting grounds within the park for nearby Dayak Villages and that sun bears are often killed with an average of ca. 10 - 20 bears taken/year in the general region (see section 5.22 on Human Activity), bear sign frequencies in this area were the highest of all the study sites. Because this area is considered one of the most important sources of animal protein for local villages, habitat protection is strong and disturbance such as logging is non-existent in the interior.

Although some highly-productive secondary forests were available adjacent to disturbed areas in all study sites, bear use of such edge habitats and ecotones was minimal up to 3,000 m from major disturbances, such as conventional logging or forest clearing for agriculture, and did not reach levels equivalent to remote primary forests until > 10 km from such disturbances. At the 10 – 100 m section levels, habitat use by bears was significantly greater as distance from disturbance edge increased (Log Likelihood X^2 =1793.901, df=l, P<0.0001) and it did not approach low to moderate levels until at least 3 – 4 km from heavily disturbed areas. Results of a general linear model (GLM) at this micro-site level were similar (r²=0.593, F= 895.08, df=50, P < 0.0001). At the transect level, GLM tests of transect means illustrated the same, but more significant relationship (r²=0.671, F=25.21, df=22, P<0.0001).

Regression models revealed disturbance distance was an important effect on bear sign presence (figures 5.6 A-B), but the GLM showed the most significant interactive effect was age of, and distance to, the disturbance relative to where and when bears were in an area $(r^2 = 0.755, F=1279.45, df=74, P<0.0001)$ (figure 5.6C). The majority of signs (92.7%) were in areas that had never been disturbed (figure 5.7). Only 6.8% of signs were observed near disturbed areas, such as logging of more than 2 – 3 trees, where 93.6% of these signs were generated by bears *prior* to when disturbance occurred. About 90% of post-disturbed signs were in areas > 100 m from the disturbance, while 86% were > 500 m and about 74% were > 1,000 m. The majority of post-disturbed signs were in secondary forests > 20 years old. No signs were observed in highly disturbed areas, such as cleared forest of < 1 year old. Only 0.32% of all signs (n=16) were observed in forest edge habitat within 10 m of a disturbed area < 1 year old and 2% of signs (n=102) were observed 50 m from the edge of forest bordering disturbed areas < 1 year old. Figure 5.7 shows the relationship between observed sign abundance and distance from disturbance in pre- *versus* post-disturbed areas.



Figure 5.6. (A) Regression of mean bear signs/ha vs. disturbance distance averaged at the transect level (1,000 m) (B) Regression of square-root transformed values of total signs/ha vs. disturbance distance at the observation level (10 m). (C) GLM plot of observed vs. predicted values of total sign abundance as affected by disturbance distance, type, and age. There is a strong relationship between the frequency of signs and distance from the disturbance, especially if disturbance is young relative to where and when bears are active in an area. As time when disturbance occurred increases, the importance of distance from that disturbance decreases. Note: Regression line in plot (C) added for graphic visual aid.



Figure 5.7. Plot of percent bear signs observed in undisturbed sites *versus* signs in postdisturbed areas. The amount of signs increased as distance from disturbance increased.

When forests were allowed to regenerate without new perturbation, the relative importance of distance from disturbed areas decreased for bears, where older secondary forests > 22 - 25 years old showed low to moderate levels of bear activity. However, bear sign frequencies were at least 2 - 4 times greater in primary forest than in any other habitat type (r²=0.685) with the next highest frequency, which was secondary forest > 22 years old. Bear activity was significantly less when < 3 - 4 km from younger forest stages.

Food is extremely important for bears, but total forage abundance was not a significant effect on bear sign variance ($r^2 = -0.0000$, df=1, P=0.9742). When examined relative to disturbance, bear sign abundance showed a contrasting trend, in that significantly lower sign frequencies ($r^2=0.723$, F=1635.2, df=49, P<0.0001) corresponded to higher total forage abundance in more disturbed areas ($r^2=0.219$, F=166.011 df=49, P<0.0001) (figure 5.8). The Aras Napal area in the eastern plain of the Leuser Ecosystem ranked highest in the study in available bear forage in lowland forests < 500 m asl, but bear sign frequency there was the lowest in the Sumatran study region, with only 3.75 signs/ha. This area is composed of young secondary forests < 25 years old surrounded by extensive forest clearing, commercial agriculture (primarily consisting of palm oil plantations), local fruit gardens, villages, roads, extensive human activities, and hunting.



Figure 5.8. Relationship between sign frequency and total forage abundance. Primary undisturbed forests had the highest sign frequencies, but moderate forage abundance. In contrast, higher forage abundances were observed in secondary forests and edges, but these areas showed very little bear activity. PF=primary forest; RIL=Reduced Impact Logging; CNV=Conventional Logging practices.

Ten kilometres further interior in Gunung Leuser National Park, the Gunung Runtuh lowland forest also ranked considerably high in available forage, but bear sign frequencies were again very low at 9.5 signs/hectare. These forests are less accessible to people and, consequently, wildlife are less vulnerable than in adjacent Aras Napal. However, the area consists of young secondary forests < 22 years old with small habitat disturbances (< 25% of observed area disturbed) and persistent human activities by local poachers for gaharu, swiftlet nests, damar, wildlife, and fish. In addition, notable logging activity was present within 4 - 5 km north of the survey area just north of the border of North Sumatra and Aceh.

The highest available forage between Sumatra and East Kalimantan was in the remote Tankahan area of Gunung Leuser National Park in mid-elevation forest, but there was a low mean bear sign frequency of 13.58 signs/ha. This survey area was within 10 - 12 km of small villages and there was persistent human activity along trails, in addition to moderate degrees of animal and tree poaching, forest clearing for gardens, village expansion, trails, roads, and so forth bordering the area.

5.13 Distance (Line-transect) Sampling

There were no known violations of assumptions for Distance sampling. Analyses of Distance modelling in programme DISTANCE showed that the best model fit for the data at the general habitat level (n=9 habitat types) was the Half-normal Simple Polynomial model (AIC=66640.40). When comparing bear sign detections at finer geographic resolutions relative to specific local habitat types and disturbances (n=50) the Hazard-Rate Cosine model fit the data best (AIC 66528.61). Both models were robust, possessing good properties for detection and model shape (Buckland *et al.* 2001). Figures 5.8 – 5.10 show probability and detection function plots for all data combined (fig. 5.8), pre-disturbed and post-disturbed signs (fig. 5.9), and signs in primary and secondary forests of all ages (fig. 5.10). When examined at the habitat level, there was a small degree of observation clustering near the transect centres as seen in the probability plots, but this is normal (such that g(0)=1) (Buckland *et al.* 2001) and the majority of the data fit the models well.

Significantly higher bear sign frequencies, density probabilities, and sign densities per unit area were in undisturbed sites regardless of habitat type, with a mean estimated sign density/ha 5.6 times greater than in post-disturbed areas (table 5.10). The probability of observing signs was higher in pre-disturbed areas, but encounter rates were significantly lower in areas before disturbance (table 5.10). Signs in post-disturbed sites and areas affected by disturbance were most often observed in clusters within specific areas. Field observations revealed that low encounter rates may coincide with more dispersed activity, especially in large contiguous forest areas, whereas higher encounter rates may be associated with sign clustering or aggregation, particularly in fragmented habitats and/or smaller patches.

Table 5.10. Overall line-transect modelling results of general habitat types (n=9) between pre-disturbance *vs.* post-disturbance bear sign densities using the half-normal simple polynomial model (AIC=66667.11). Note that modelled sign densities reflect the estimated densities and are not absolute density figures.

	Pre- Disturbed Areas	Pre-Disturbed 95% Confidence Interval	Post- Disturbed Areas	Post-Disturbed 95% Confidence Interval
Bear Sign Density per hectare	12.92	11.083 - 15.053	2.37	1.8741 - 2.9993
Density Probability <i>f</i> (0)	0.19434 ^{E-02}	$0.18422^{E\text{-}02} - 0.20501^{E\text{-}02}$	0.15215 ^{E-02}	$0.14492^{\text{E-02}} - 0.15974^{\text{E-02}}$
Encounter Rate n/L	0.13293 ^{E-01}	$0.11515^{\text{E-01}} - 0.15345^{\text{E-01}}$	0.31165 ^{E-01}	$0.24758^{\text{E-02}} - 0.39230^{\text{E-02}}$



Figure 5.8. Best fitting models in DISTANCE for: (A) Detection probability plot of all sun bear sign data (AIC=66699.38), (B) Quantile-quantile distribution function plot of sun bear signs in pre-disturbed areas (AIC=66667.11), and (C) Quantile-quantile distribution function plot of sun bear signs in post-disturbed areas (AIC=66667.11). All three plots were best fit by the Half-Normal Cosine model according to AIC values.



Figure 5.9. Best fitting models of sun bear sign in primary forests plotted by the Half-normal Simple Polynomial model in DISTANCE (AIC=66640.40). (A) Detection probability plot and (B) Quantile-quantile distribution function plot Note: as expected there is a small spike in data near the centre line, while the majority of data fit very close to the line.



Figure 5.10. Best fitting models of sun bear sign in secondary forests plotted by the Half-normal Simple Polynomial model in DISTANCE (AIC=66640.40). (A) Detection probability plot and (B) Quantile-quantile distribution function plot. As expected, there is a spike in data near the centre line, but the majority of data fit very close to the line.

In general, the Distance sampling method was found to be more robust than Fixedwidth censusing because it estimated density by accounting for the probability of unobserved signs as distance from the transect centre increased, whereas Fixed-width censusing assumed all signs within the strip were recorded. Nevertheless, these two methods resulted in similar patterns and Distance modelling corroborated the statistical results of Fixed-width censuses. In DISTANCE, the Half-normal model at the general landscape level and the Hazard-rate model at more fine resolutions of habitat and disturbance types validated Fixed-width census result patterns and demonstrated clearly that the significant majority and densities of sun bear signs were in undisturbed primary low- to mid-elevation forests (400 - 750 m asl)followed by primary forest ridge tops < 1,000 m asl, and primary montane forests < 1,200 m asl respectively (figure 5.11A). Note that these are not absolute densities; rather, they are modelled estimates based on probabilities of signs being detected and missed along the transect. The next highest sign density estimates were found in secondary forests > 20 - 25years old and in undisturbed swamp habitats. DISTANCE models showed that estimated sign densities were significantly reduced along trails, RIL-logged (Reduced-Impact Logging) primary forests, 15 - 20 year old secondary forests, and edge habitats respectively.

When biogeographic parameters, such as elevation, aspect, slope, tree stand character, forage abundance, and so on, were added to the models as covariates, the same pattern emerged. Essentially, as the level of disturbance in surveyed areas increased, the detection functions, sign densities, and abundances all declined to the point where young secondary forests < 10 years old, agricultural areas, CNV-logged areas (Conventional Logging), exposed edge habitats, high-use human trails, and logging roads all displayed extremely low or zero probabilities of detection and, subsequently, minimal to no sign.

Plotting the DISTANCE modelled data on a logarithmic scale illustrates the large difference in the relative densities of estimated sign/hectare as disturbance intensity increases (figure 5.11B). This plot shows that estimated bear sign densities in young secondary forests < 10 years-old, agricultural areas, and highly-disturbed areas are proportionally about 1,000 times smaller than in undisturbed primary lowland and mid-elevation forests, such that all non-forest and disturbed areas have estimated sign densities < 1 sign/hectare. A few habitats in this graph immediately adjacent to primary forest also had low densities. These were primary montane forests > 1,200 m asl, where sign densities were much lower, especially in higher elevation moss forests.



Figure 5.11. Distance survey modelling results of bear sign densities in all habitat and disturbance types (n=50) at alpha-scale resolution using the Hazard-rate Cosine model (AIC=66528.61). Data categories are colour-grouped according to general habitat types. Plot **(A)** illustrates the significant difference between undisturbed primary forests and intensely-disturbed areas, where the vast majority of signs were in undisturbed primary forests. Plot **(B)** shows the same data on a logarithmic scale and demonstrates a 1,000-fold relative difference in the estimated density of signs between undisturbed primary forest and highly disturbed areas, such as oil palm plantations and clear-cuts. PF=primary forest; SF=Secondary Forest; RIL=reduced-impact logging; AG=agriculture; CNV= conventional logging and clear-cuts.

5.14 **Biogeographic Surveys**

Biogeographic conditions can, in some cases, strongly influence animal movements and habitat use by affecting forage type, diversity, and abundance, as well as the degree to which individuals can access those resources and compete with or prey on other species. A variety of tests were conducted to examine such biogeographic influences on sun bear habitat use. General Linear Models, Logistic Regression, Linear Regression, Chi-square, Odds Ratios, Correlations, and non-parametric tests, such as Kruskal-Wallis and the Mann-Whitney *U*, were all used for various parameters and their interactions.

General Linear Models (GLM) were first used to examine the interactive effects of all 15 biogeographic variables combined on sun bear sign frequency, regardless of site or transect. Because topographic variation in these areas can change dramatically over distances of < 10 m, the first model tested error variance in bear sign frequency relative to potential effects of slope, aspect, and elevation at the original level of measurement every 10 m along transects. Significant differences were found, but only a small amount of error in bear sign frequency was estimated ($r^2=0.162$, F=396.04, df=15, P<0.0001). The next model parameters included canopy cover, ground cover, escape cover (refugia), slope, aspect, elevation, proximity to water sources, and primary sun bear forage abundances of fruit, termite colonies, ant colonies, bee hives, and other forage, such as non-fruiting *Ficus* spp.. In this model, significant differences were observed between areas of bear sign abundance (r²=0.494, F=631.14, df =27, P<0.0001). By far the most dominant factors were elevation, refugia, and fruit respectively. Only one parameter, the abundance of bee hives, was insignificant (P=0.0733) in this model. Slightly more variability in bear sign abundance was explained when competitor and predator presences were added to the model ($r^2=0.499$, F=598.70, df = 29, P<0.0001), but bee hive abundance remained the only insignificant effect (P=0.0731). Variables most correlated with high sign abundance were refugia (Pearson's r = 0.649), canopy cover (Pearson's r = 0.551), and elevation (Pearson's r = 0.368).

When controlling for habitat and disturbance differences, much more variability in bear sign was explained, particularly at finer (alpha) scales of resolution, where the highest frequencies of bear signs were in undisturbed primary forest. The final model was highly significant (r^2 =0.786, F =775.42, df = 82, P<0.0001), in which bee hive abundance became a significant effect in this model, while the presence of antagonistic species (P=0.953), competitors (P=0.782), and distance to water (P=0.98) were the only insignificant effects. Figure 5.12 illustrates the differences in observed *versus* predicted values in the biogeographic GLM models without (fig. 5.12A) and with disturbance (fig. 5.12B) as an interactive effect.



Figure 5.12. Plots of observed *versus* predicted values of total sign abundance as affected by biogeographic variables (A) and with habitat disturbance as an interactive effect (B). A significant amount of error in bear sign frequency was explained with disturbance as an interactive effect. Note: Regression lines added for graphic visual aid.

Independence among these types of variables (e.g. synchronous fruiting, topography, etc.) between adjacent 10 m sections is unlikely and could influence results. Thus, the mean of each variable was calculated in SAS (SAS 2003) for each transect and a stepwise GLM was conducted at the transect level (i.e. grouped sampling units of 1,000 m) rather than among 10 m sections. Beginning with general macro-habitat level differences, I then added transect means for each biogeographic variable and tested potential effects on bear sign frequency.

At the transect level, bear sign frequencies were significantly different among general habitat types, such that the highest frequencies were observed in undisturbed primary forest followed by swamp and then secondary forest ($r^2=0.541$, F=37.25, df=9, P<0.0001).

The second variable added was canopy cover, which helped explain slightly more variance in bear sign frequency in the overall model ($r^2=0.576$, F=38.66, df=10, P<0.0001) (habitat type: F=12.53, df=9, P<0.0001; canopy cover: F=24.14, df=1, P<0.0001). Once all biogeographic variables were added to the model, the only parameters that showed any significant effects were: habitat type, elevation, escape cover, competition, and the availability of alternative forage dominated by non-fruiting *Ficus* spp. trees ($r^2=0.739$, F=24.4, df = 27, P<0.0001). All insignificant parameters were removed and the final model showed that general habitat type, elevation, escape cover, and possible competition explained almost 73% of the error variance in bear sign frequencies across all transects ($r^2=0.728$, F=54.79, df=13, P<0.0001). In this case, the most prominent effect was elevation, followed by escape cover, and then general habitat type respectively.

As a control, the same habitat types within primary forests were examined. Results showed that total sign was significantly different at the 10 m level relative to most biogeographic variables ($r^2=0.206$, F=584.03, df=9, P<0.0001). The most significant differences were attributed to the percent canopy and ground covers, refugia level, elevation, and abundance of fruit and bee hives, but very little variance (20%) in total bear sign was explained. At the transect level (1,000 m), slightly more variance in total bear sign was clarified (figure 5.13) ($r^2=0.261$, F=8.09, df = 8, P<0.0001), but the only significant effects were the degree of canopy cover (F=5.98, P<0.0154) and refugia (F=6.78, P<0.0100). Thus, canopy and escape covers appeared to be the most dominant effects on sign frequency in primary forest.



Figure 5.13. Plot of observed *versus* predicted values of total sign abundance in primary forests as affected by biogeography. Little variance was explained other than by elevation and cover.

When testing the interactive effects of disturbance with biogeography on bear sign frequencies at the 10 m level across all sites, disturbance appeared to be the most significant effect across transects by increasing the explained variance from < 50% to almost 80% (r^2 =0.794, F=1333.52, df = 89, P<0.0001). A GLM was then used to test grouped mean differences among disturbance treatments at the 1,000 m transect level. The same procedure was used, such that disturbance was first tested in isolation against mean bear sign frequencies/transect and then each biogeographic variable was added in succession in the same order as the first model.

Transect-level results showed that mean bear sign frequencies were significantly different among habitats ($r^2=0.655$, F=24.10, df=21, P<0.0001). The highest sign frequencies were observed in undisturbed mid-elevation (500 – 750 m asl) and ridge-top primary forest, followed by undisturbed primary lowland forest (< 500 m asl) and then secondary forest > 20 – 25 years. Again, slightly more variance in bear sign frequency was explained in the overall model when canopy cover was added ($r^2=0.675$, F=24.93, df=22 P<0.0001); disturbance: (F=10.16, df=21, P<0.0001; canopy cover: F=15.52, df=1, P=0.0001). When all biogeographic variables were added to the model, the only parameters showing significant effects were: disturbance, elevation, and refugia ($r^2=0.785$, F=22.54, df = 38, P<0.0001). All insignificant parameters were removed and the final model showed that disturbance, elevation, and refugia explained 76% of the error variance in bear sign frequencies ($r^2=0.761$, F=35.8, df=24, P<0.0001). The most prominent effect was disturbance, followed by elevation and then refugia. Disturbance had a strong negative correlation (Pearson's r = 0.515), where bear activity was most correlated with undisturbed primary forests (Pearson's r = 0.624) and increased as distance from disturbance increased (Pearson's r = 0.511).

In general, biogeography is significantly different relative to sun bear sign frequency, where higher sign frequencies were associated with older more heterogeneous primary forest traits, such as high canopy cover (>95%) and refugia (> level 3), low ground cover (<20%), high tree species diversity, and mature stand structure. Particular traits are summarised in more detail in proceeding sections, including correlations among these variables. Elevation and cover were the most important biogeographic effects, but the most significant influence in these models was the interactive effect of habitat disturbance, which accounted for the majority of variance in bear sign abundance among sites.

5.15 Tree Stand Character

5.15a General Stand Traits

Tests were performed to examine the hypothesis that tree stand characteristics are potentially important factors determining sun bear habitat use. Results of tree stand surveys along 20% stratified-random samples of 100 m sections on each transect indicated that tree stand traits were prominent effects in micro-site and habitat type selection by sun bears. Tree densities were moderately higher by 6% (Mann-Whitney U=7.685, P<0.0001), whereas other physical stand traits, such as tree maturity, girth (dbh), basal area, height, number of emergents and crown trees, and canopy cover were all significantly higher in those stands with significantly more bear activity (r²=0.735, F= 1551.71, df=11, P<0.0001). Pearson correlations showed that a higher number of emergent trees (Pearson's r = 0.315) along with more fruit productivity (Pearson's r = 0.412) were the strongest parameters associated with high frequencies of bear signs in individual 100 m sections.

Such selection by the bears indicated a strong preference for older forest character, and 93.2% of all signs were observed in undisturbed primary forest with a high degree of stand maturity and diversity ($r^2=0.7223$, F=1635.2, df=49, P<0.0001). Regardless of whether analyses were limited to the 10 m wide transect strip or across the full width of the survey during Distance sampling measures, there were ten-fold more signs in 100 m sections with these stand traits. A predominance of mature trees, fruit availability and high tree species diversity (see below) were strongly associated with bear activity and were important indicators of site affinity of the bears. Surveys were conducted throughout the year, yet 100 m sections with more bear signs had significantly higher abundances of fruit (Log Likelihood $X^2=61.78$, P=0.001). Sections with fewer signs had 50% more tree flowering without fruit (Log Likelihood $X^2=87.454$, P<0.0001). When comparing sections with equal amounts of signs, most stand traits were relatively moderate in character, falling between the two extremes.

5.15b Tree Diversity

Tree species diversity differences among habitat and disturbance types were tested using PISCES Species Diversity and Richness III software (version 3.03) (Pisces 2002). Table 5.11 shows the results of various alpha-level diversity indices based on general habitat types. Indices were based all trees \geq 10cm dbh within the 10 m wide strip of two 100 m random sample sections along every transect. A total of 590 one-hundred metre sections from 295 km of transects were analysed. Primary forest had 3.2 times more tree species than

the next closest habitat type, secondary forest. Bootstrap randomisation tests (Solow 1993) for every diversity index across all habitat and disturbance types consistently showed that primary forest was significantly more diverse in tree species than any other habitat type. The Berger-Parker Dominance index also showed that primary forests were highly heterogeneous with extremely low dominance by particular tree families or species. The Rényi diversity ordering index (figure 5.14) demonstrated that primary forest was consistently the most diverse, followed by secondary forest, edge, swamp, and montane habitats. But, secondary forest is potentially uncomparable with the latter habitats because its index crosses those of edge and swamp habitats in both the Rényi and K-Dominance measures. In terms of abundance, the K-Dominance index resulted in ranked diversities similar to all of the other indices, such that primary forests were highly heterogeneous with relatively few species and genera dominating (figure 5.15).

When examined at finer resolutions defined as 38 different habitat and disturbance types, similar results were found (table 5.12). Essentially, the diversity indices, diversity ordering, and K-dominance scores all showed that primary undisturbed forest habitats were consistently the most diverse and heterogeneous areas for tree species surveyed in both North Sumatra and East Kalimantan. In this case, primary lowland forest had at least 4.1 times higher tree species diversity than the next highest habitat type, which was 20+-year-old secondary forest.

Table 5.11. Six of the most important alpha-diversity indices for tree species diversity across the main habitat or disturbance types in East Kalimantan and northern Sumatra. Indices are based on data generated from all trees \geq 10cm dbh within the 10 m wide strip of two 100 m random sample sections along every transect. A total of 590 sections from 295 km of transects were measured. Bootstrap randomisation tests for every index showed that primary forest was significantly more diverse in tree species than any other habitat type.

General Habitat or Disturbance Type	Number Trees Species	Shannon- Wiener <i>H</i> Index	Simpson's D Index	Margalef <i>D</i> Index	Berger- Parker Dominance Index	Fisher's Alpha Index
Primary Forest	1730	6.191	245.1	176.5	0.02362	471.7
Secondary Forest	546	5.293	100.9	62.52	0.06236	145.2
Edge	232	5.08	143.9	35.07	0.01931	118.0
Montane Forest < 1,200 m asl	135	4.185	33.44	20.71	0.113	51.97
Swamp	127	4.493	80.0	20.24	0.03357	54.49
Montane Forest > 1,200 m asl	41	2.965	12.46	6.916	0.1631	12.41
Closed Logging Road	30	2.971	15.88	6.947	0.1846	21.61
Local Gardens	4	1.277	5.25	1.542	0.4286	3.879
Plantations	2	0.6581	1.966	0.03396	0.6316	0.5635

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Figure 5.14. The Rényi diversity (Rényi, 1961) ordering index is based on Na for a = 0, 1, 2 and gives the total species number, Shannon-Wiener H, and Simpson's D respectively. By varying 'a' there will be range of diversity measures. To test for non-comparability of communities Ha is calculated for a range of a values. If a community is always greater it is considered to be more diverse. If two communities cross over they are non-comparable (Pisces 2002). According to this index, primary forest was consistently the most diverse, followed by secondary forest, edge, swamp, and montane habitat. Note that secondary forest crosses edge and swamp habitats.



Figure 5.15. The K-Dominance index of species diversity is the percentage cumulative abundance plotted against log species rank (Lambshead *et al.* 1983). The lower line has the highest diversity and if the lines for two samples cross they usually rank differently for different diversity indices. Again, primary forest ranked highest, followed by older secondary forest, edge, lower montane forest < 1200 m asl, and swamp. Again, the secondary forest index crosses those of swamp and edge habitats.

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Table 5.12. Six of the most important diversity indices for tree species diversity for the main habitat or disturbance types at alpha-resolution in East Kalimantan and northern Sumatra.

General Habitat or Disturbance Type	Number of Tree Species	Shannon-Wiener <i>H</i> Index	Simpson's D Index	Margalef D Index	Berger-Parker Dominance Index	Fisher's Alpha Index
Primary Forest lowland < 500 m asl	1147	5 935	211.5	132.2	0.0150	322.2
Primary Forest mid-elev 500 – 1000 m asl	506	5 565	178.6	62.98	0.0197	173.3
Primary Forest CNV logged > 10 years	342	4.841	44.45	47.54	0.1113	151.0
Secondary Forest 20 years old	279	4,797	75.44	37.00	0.0404	91.66
Secondary Forest 22 years old	232	4.865	99.12	29.74	0.0335	63.71
Primary Forest Ridge	164	4.285	38.29	24.17	0.1106	60.47
Primary Forest with Reduced Impact Logging 5 years earlier	161	4.157	25.98	25.08	0.1441	72.96
Primary Forest between 150 – 1150 m from orange grove	151	4.046	17.26	21.46	0.2210	47.63
Secondary Forest Edge 23 years old bordering orange grove	129	4.531	86.29	21.13	0.0304	62.79
Primary Forest Swamp	127	4.493	80.00	20.24	0.0356	54.49
Primary Montane Forest < 1200 m asl	124	4.211	39.45	19.71	0.1053	51.96
Primary Forest CNV logged < 10 years	119	4.089	37.21	19.41	0.0938	53.85
Secondary Forest 23 years old between 150 – 1150 m from local fruit gardens	113	4.228	43.24	19.23	0.0947	59.49
Primary Forest between 150 – 1150 m from hill rice swidden	83	4.131	62.12	15.64	0.0582	56.50
Primary Forest Ridge Trail	69	3.882	44.12	13.14	0.0678	41.58
Primary Forest CNV logged 9 years earlier	65	3.726	32.58	12.34	0.0949	36.70
Primary Edge Forest adjacent to hill rice swidden	62	3.736	36.53	12.08	0.0769	38.06
Secondary Forest 20 years old between 150-1150 m from oil palm plantation	58	3.840	48.68	12.06	0.1062	47.83
Primary Montane Moss Forest < 1200 m asl	47	3.055	8.506	9.406	0.3308	25.92
Primary Forest Swamp	44	3.471	29.52	8.951	0.123	24.69
Secondary Forest 15 years old	41	3.439	32.50	8.867	0.0989	28.72
Primary Montane Moss Forest > 1200 m asl	41	2.965	12.46	6.916	0.1631	12.14
Secondary Edge Forest 23 years old adjacent to oil palm plantation	39	3.337	23.46	8.857	0.1781	34.05
Primary Forest river edge CNV logged < 10 years earlier	33	3.296	32.14	7.558	0.1014	24.81
Secondary Forest 25 years old	30	2.689	7.959	6.545	0.3214	16.69
Secondary Forest 10 years old	29	3.046	18.08	6.758	0.1905	20.82
Closed logging road CNV logged 10 years earlier	28	3.020	20.40	6.833	0.1538	24.73
Primary Forest Swamp CNV logged < 10 years earlier	24	2.816	13.93	5.941	0.2292	19.10
Secondary Forest 8 years old	24	2.691	12.09	5.51	0.1846	13.75
Secondary Forest 10 years old	21	2.462	7.348	4.74	0.3382	10.39
Secondary Forest river edge CNV logged < 5 years earlier	15	2.372	9.894	4.077	0.2581	11.44
Secondary Forest 5 years old	3	0.898	2.50	0.8686	0.60	1.453
Local Fruit Garden	2	0.562	2.0	0.7213	0.75	1.592
Closed logging road CNV logged < 5 years	2	0.271	1.182	0.3899	0.9231	0.659
Local Garden (Bananas)	1	0	1	0	1	0
Hill Rice Swidden	1	0	1	0	1	0.796
Orange Plantation	1	0	1	0	1	0.319
Palm Oil Plantation	1	0	1	0	1	0.259

5.15c Bear Trees

Trees used by sun bears (i.e. those trees with positively-identified bear sign(s)) reflected a very similar pattern to overall tree diversity among habitat and disturbance types. Table 5.13 shows a total of 772 different tree species that were used by sun bears. East Kalimantan had 608 species and North Sumatra had 187 species. Sign tree dbh averaged 43.74 cm (range: 3.25 - 926.43 cm) and height was 18.37 m (range: 1 - 55 m). Sign sites had a canopy cover of 95.8% and ground cover 16.9% on a slope of 24.16⁰ and elevation of 420 m asl. Sign trees were taller in Sumatra, but broader in East Kalimantan.

Table 5.13. Tree species used by sun bears ("bear trees") by region, focal area and study site. Note: some species will occur within the same focal area and/or ecosystem. Thus, individual site totals summed as "Total Different Species" are different than the overall total of species used by bears ("Total Used Species").

Region	Total Tree Species	Focal Area	Total Tree Species	Study Site	Total Tree Species
				South Seturan Undisturbed Primary Forest	139
	608			Seturan Primary Forest RIL/CNV Logged	122
		East Bulungan	279	Tukuk Mawot Undisturbed Primary Forest	66
East Kalimantan Borneo				Gunung Sidi/Loreh Primary Forest CNV Logged	46
		Kayan		Ulu Stee	133
		Mentarang	264	Lalut Birai	113
		National	201	Jalungkereng	105
		Park		Nnggeng Tau	94
		West Bulungan		Bahau River Undisturbed Primary Forest	96
			176	Bahau River Secondary Forest	48
				Alango Secondary Forest	67
		Gunung Leuser	1.50	Sei Badak	117
		National Park East Slope	158	Tankahan	82
North Sumatra		Gunung Leuser	07	Gunung Runtuh Secondary Forest	70
Sumatra	187	East Plain	21	Sekundur Secondary Forest	41
		Aras Napal	16	Aras Napal Disturbed / Cleared Secondary Forest	16
Total Used Species	795		990		1,355
Total Different Species	772		772		772

Widely-distributed tree species that were common to multiple areas were selected by bears at different sites, which is noted as 'Total Used Species' in table 5.13. For example, on a regional level there were 23 tree species used by bears that were common to both East Kalimantan and North Sumatra, but on a site level common species were dominant. At this level ca. 583 species were selected by bears multiple times across sites, reflecting relative importance of particular families and genera. Some of the most dominant species selected multiple times by sun bears belong to the families Dipterocarpaceae, Euphorbiaceae, Fagaceae, Lauraceae, Moraceae, Myrtaceae, and Sapindaceae.

The most diverse area was in primary forests of East Bulungan with 279 different tree species used by bears, followed by Kayan Mentarang National Park with 264 selected tree species. The next most diverse site was in West Bulungan along the Bahau River adjacent to Kayan Mentarang National Park. Bears in this area used 176 different tree species, of which primary forest had at least 50% more species used by bears than secondary forest and disturbed areas. The less disturbed east slope region (Tankahan and Sei Badak) of Gunung Leuser National Park showed the highest bear tree diversity in the Sumatran sites with 158 species. The adjacent east plain area (Gunung Runtuh, Sekunder) had 98 selected species and the highly-disturbed area of Aras Napal had only 16 tree species showing bear signs.



Figure 5.16. The Rényi diversity (Rényi, 1961) ordering index for trees selected by sun bears showing signs. **Note:** sample sizes in swamp areas were quite low and may not reflect true diversity levels in that habitat type.

Primary lowland (< 500 m asl) and mid-elevation (500 - 1,000 m asl) forests were at least 3 - 4 times higher in their diversity of trees used by sun bears than in the next highest habitat, which was low-impacted secondary forest > 20 years old that retained a large portion of primary forest traits (table 5.14). Interestingly, diversity indices for bear trees in these old secondary forests were similar to primary forest ridges. The heterogeneity of selected trees, such as varying height, girth, maturity, etc. was quite important, revealing that mature stands were predominantly used and most diverse in character. All five of the main diversity indices (Shaanon-Wiener *H*, Simpson's *D*, Margelef *D*, Berger-Parkar Dominance, and Fisher's Alpha) (PISCES 2002), the Rényi diversity ordering (figure 5.16), and *K*-Dominance scores showed that the highest diversity and heterogeneity of trees selected by sun bears were in primary forests.

Relative to disturbance, undisturbed primary forests were almost 5 times more diverse in bear-selected trees than in adjacent forests that sustained some primary forest traits, but that were conventionally logged > 10 years earlier. It is important to note that for a predominantly frugivorous tropical species like the sun bear, high tree species diversity provides a greater degree of potential fruit availability, density, and abundance across the landscape. This can be critical during asynchronous fruiting cycles or stochastic events, such as E1 Niňo Southern Oscillation (ENSO) events.
Table 5.14. Bear Trees. Six of the most important alpha-diversity indices for tree species used by sun bears ("bear trees") for main habitat or disturbance types at macro-scale resolutions in East Kalimantan and northern Sumatra.

General Habitat or Disturbance Type	Number of Species	Shannon- Weiner <i>H</i> Index	Simpson's D Index	Margalef D Index	Berger-Parker Dominance Index	Fisher's Alpha Index
Primary lowland Forest < 500 m asl	437	5.40	115.20	58.64	0.05	190.70
Primary mid-elevation Forest 500-100 m asl	334	4.91	58.23	45.39	0.08	131.50
Secondary Forest 20 years old	107	4.18	41.82	18.68	0.10	61.09
Primary Forest Ridge	96	4.10	46.95	16.47	0.06	46.49
Primary Forest CNV logged > 10 years earlier	94	4.19	53.37	18.03	0.09	83.43
Primary Forest Ridge Trail	37	3.32	25.37	8.62	0.17	35.65
Primary Forest reduced impact logging < 5 years earlier	36	3.38	36.67	8.70	0.13	43.53
Primary Forest CNV logged 10 years earlier	33	3.14	20.83	7.64	0.15	26.26
Secondary Forest 22 years old	33	3.13	20.07	7.39	0.16	22.19
Primary Forest (150 – 1150 m from hill rice swidden)	31	3.19	28.49	7.67	0.12	34.82
Primary Edge Forest adjacent to hill rice swidden	29	2.89	11.46	6.78	0.27	21.22
Primary Forest Swamp	20	2.77	18.21	5.43	0.21	21.51
Secondary Forest 15 years old	15	2.62	31.67	4.67	0.15	27.26
Primary low montane Forest < 1200 m asl	13	1.89	4.16	2.90	0.46	4.97
Primary Forest CNV logged 9 years earlier	11	2.30	21.00	3.69	0.20	18.60
Secondary Forest 10 years old	10	2.25	33.00	3.62	0.17	28.23
Secondary Forest 23 years old (150 – 1150 m from orange grove)	10	2.20	13.91	3.11	0.22	9.27
Hill Rice Swidden	9	1.95	8.08	2.95	0.33	9.50
Secondary Forest 25 years old	9	1.80	5.39	2.63	0.38	5.97
Secondary Forest 8 years old	9	2.08	12.00	2.89	0.25	8.51
Primary Forest Swamp CNV logged < 10 years earlier	7	1.52	3.71	2.34	0.54	6.18
Primary Forest River Edge	7	0.85	1.57	1.69	0.80	2.63
Closed Logging Road < 10 years earlier	4	1.28	5.25	1.54	0.43	3.88
Secondary Forest Swamp	4	1.33	10.00	1.86	0.40	9.28
Secondary Edge Forest 23 years old adjacent to oil palm plantation	3	1.10	3.00	1.82	0.33	3.00
Secondary Edge Forest 23 years old adjacent to local fruit gardens	3	0.95	3.33	1.24	0.60	3.17
River Edge CNV logged < 10 years earlier	2	0.69	2.00	1.44	0.50	2.00
Secondary Edge Forest 23 years old adjacent to orange grove	2	0.69	2.00	1.44	0.50	2.00
Secondary Forest 23 years old (150 – 1150 m from oil palm plantation)	2	0.69	2.00	1.44	0.50	2.00
Salt Lick/Pool	2	0.69	2.00	1.44	0.50	2.00

5.16 Primary Forage

Animal movements, home ranges, behaviour, health, survival, and fitness can be strongly influenced by the abundance, diversity, availability, and location of primary forage. Scat analyses showed that the main components of the sun bear's diet in these sites were fruit (85%), bee hives (10%), termites (3%), and ants and other insects (<1%), which correlated with the frequency of different bear signs. These and other bear food items were recorded each metre along all transects and were analysed for their occurrence and frequency relative to bear habitat use. All food items were also combined as one variable, "Total Forage", and were modelled in the forage Relative Abundance Index to estimate the importance of overall food item frequency, diversity, and coverage relative to bear activity and habitat use.

5.16a Total Primary Forage

Forage cover ($\overline{x} = 1.98 \pm 0.0035$ SE) along all transects had a weak negative correlation with sign frequency (Pearson's r = -0.047). Cumulative abundances of all food items combined as one variable, "Total Forage", showed no significant differences among transects and also had a weak negative correlation (Pearson's r = - 0.00018) with bear sign frequency. When isolating Total Forage according to general macro-habitat types, significant differences were found among transects (r²= 0.547, F=34.32, df=10, P<0.0001). The highest mean forage availability was observed in undisturbed lowland swamps ($\overline{x} = 15.68$), followed by primary montane forest < 1,200 m asl ($\overline{x} = 15.61$), secondary forest > 20 years old ($\overline{x} =$ 13.27), primary upper montane forest > 1,200 m asl ($\overline{x} = 11.72$), and primary lowland forest ($\overline{x} = 11.34$). When factoring in disturbance at finer scales, more variation was explained in bear sign frequency and distribution among sites (r²=0.678, F=24.78, df=22, P<0.0001).

Tests of transect-level grouped means revealed some lowland secondary forests > 23 years old had slightly higher Total Forage abundance than adjacent primary lowland forest (r^2 =0.025, F=5.49, df=1, P<0.0001), but means may not illustrate this variable's ecological importance. Table 5.15 shows micro-habitat differences at 10 m levels, which account for more variation (r^2 =0.729, F=1656.18, df =50, P=<0.0001). Observations may not be fully independent at this scale, but the importance of forage availability for bears at micro-habitat levels can offset statistical independence. In the Tropics, seasonality and patchiness can affect the availability of each food item when a bear is foraging. For example, > 86% of transects had significantly dispersed or no core food cover (r^2 =0.295, F=37.67, df=291, P<0.0001). Thus, Total Forage may be an important measure of overall food abundance due to asynchronous and patchy bear forage across seasons, years, and habitats, where the abundance of some items at the micro-site level compensates for loss of others.

Habitat or Disturbance Type		Forage dance
Habitat of Disturbance Type	Mean	Std Dev.
Secondary Forest > 23 years old between 150 – 1150 m from local fruit garden	17.79	6.39
Secondary Forest Swamp > 23 years old	16.89	3.02
Primary Lower Montane Forest < 1200 m asl	16.38	4.93
Secondary Forest > 23 years old between 150 – 1150 m from orange grove	15.89	5.37
Primary Forest Swamp	15.69	4.91
Secondary Forest > 23 years old between $150 - 1150$ m from oil palm plantation	15.10	4.59
Secondary Forest > 22 years old	14.89	3.20
Secondary Forest Salt Lick or Pond > 22 years old	13.88	3.31
Secondary Forest > 20 years old	13.17	5.73
Primary Upper Montane Forest > 1200 m asl	13.10	4.98
Primary Forest mid-elevation 500 – 1000 m asl	12.87	5.99
Primary Lowland Forest Trail	12.69	4.10
Primary Lowland Forest Swamp	11.71	2.64
Primary Lowland Forest Wildlife Trail	11.70	3.35
Primary Lowland Forest River Edge	11.67	1.90
Primary Lowland Forest > 23 years old between 150 – 1150 m from hill rice swidden	11.62	3.04
Primary Lower Montane Moss Forest < 1200 m asl	11.60	4.65
Secondary Forest Edge > 20 years old bordering orange grove	11.45	5.21
Primary Lowland Forest	11.10	3.76
Primary Forest Ridge Wildlife Trail	10.93	2.70
Primary Lowland Forest CNV logged < 10 years earlier	10.53	3.52
Primary Lowland Forest Swamp CNV logged < 10 years earlier	10.41	2.56
Primary Upper Montane Moss Forest Wildlife Trail > 1200 m asl	10.35	2.13
Primary Forest mid-elevation Wildlife Trail 500 – 1000 m asl	10.34	2.25
Closed Logging Road > 20 years old	10.20	2.12
Secondary Forest > 15 years old	10.09	2.84
Primary Forest Ridge	10.08	2.80
Primary Lowland Forest Swamp CNV logged 10 years earlier	10.04	2.59
Primary Forest mid-elevation Trail 500 – 1000 m asl	10.00	3.94
Primary Lowland Forest Swamp CNV logged 9 years earlier	9.69	3.06
Secondary Forest Trail > 10 years old	9.60	1.81
Local Fruit Gardens (various fruits)	9.52	3.12
Primary Lowland Forest with reduced impact logging 5 years earlier	9.44	2.27
Primary Forest Ridge Trail	9.25	2.25
Primary Forest Edge bordering hill rice swidden	9.19	3.44
Orange Grove	9.08	3.44
Secondary Forest Trail > 20 years old	8.60	2.59
Local Orange/Teak Garden	8.35	1.73
Local Banana Garden	8.16	1.83
Secondary Forest > 25 years old	7.86	2.33
Oil Palm Plantation	7.82	2.47
Secondary Forest > 10 years old	7.65	2.13
Secondary Forest Edge 20 years old bordering oil palm plantation	7.60	2.09
Secondary Forest < 8 years old	7.15	1.96
Hill Rice Swidden	3.75	1.61
Closed Logging Road < 5 years old	2.80	0.75

Table 5.15. Mean Total Forage abundances at 10 m alpha-scale resolution along transects.

5.16b <u>Fruit</u>

A 20% stratified-random sample of tree stands along each transect showed that 100 m transect sections with significantly more bear signs had correspondingly higher percentages of available fruit (Log Likelihood X^2 =61.78, P=0.001). The interaction between available fruit and general macro-habitat type explained more of the variation (r²=0.359, F=4.71, P=0.0004). The fruit and flower productivity index was a significant parameter, but it could not singularly explain sufficient variability in bear signs among transect sections in a GLM (r²=0.0302, F=292.58, P<0.0001). When the amount of bear signs/section was analysed relative to the fruit and flower productivity index as an interaction with general macro-habitat type (n=9 habitats), a much higher degree of variation was explained (r²=0.589, F=537.84, df=25, P< 0.0001). At a finer resolution of habitat and disturbance types (n=26 types) an even higher degree of variability could be explained with this interaction (r²=0.694, F=330.16, df=64, P<0.0001).

Fruit abundance was significantly different among general habitat and disturbance types. At the time of surveys, primary montane forest < 1,200 m asl exhibited the highest mean fruit abundance, followed by primary lowland swamps, primary upper elevation montane forest > 1200 m asl, and secondary forest > 20 years old. Although primary lowland forests were far more diverse and heterogeneous in tree species diversity and structure than all other habitat types, fruit abundance at the time of surveying was lower than in primary montane forests, swamps, or secondary forests > 20 years old. Edge, gardens, and plantations were respectively lower in mean fruit abundance.

When averaged as a mean along the entire 1,000 m of each transect, fruit abundances were also significantly different across transects. But, as with the random 100 m section surveys noted above, the transect-level means could not explain sufficient variability in bear signs across transects (r^2 =0.0047, F=147.32, df=1, P<0.0001). At a general macro-habitat level significantly more variation could be explained (r^2 =0.524, F=2000.43, df=1 0, P<0.0001), and at a finer resolution of habitat and disturbance types (n=50) the most variation could be explained (r^2 =0.744, F=913.67, df=37, P<0.0001). The geographic coverage of available fruit along transects was also a significant effect at both the general habitat level (r^2 =0.525 F=2001.88, df=10, P<0.0001) and the micro-habitat/disturbance level (r^2 =0.742, F=932.33, df=37, P<0.0001).

5.16c Termite Colonies

Although scats did not contain large amounts of termite remains, observations of termite colony foraging and association with bear signs showed that termites are a frequently used food item by sun bears. GLM tests for visible termite colonies showed that there was a significantly higher abundance of termite colonies where there were more bear signs. However, termite colonies alone could not explain sufficient variability in bear sign frequency among transects ($r^2=0.074$, F=2463.33, df=1, P<0.0001). When isolating general macro-habitat types significantly more variation could be explained ($r^2=0.509$, F=3561.67, df=9, P<0.0001), and at a finer resolution of habitat and disturbance types (n=50) the most variation could be explained ($r^2=0.723$, F=1607.21, df=50, P<0.0001). The highest frequencies of bear signs were associated with higher abundances of termite colonies, which were in undisturbed primary forests, followed by primary forest edge, primary forest ridge tops, closed logging roads with > 5 years regeneration, secondary forest > 20 years old, and then swamps. The geographic coverage of available termite colonies along transects was also a significant effect at both the general habitat level ($r^2=0.515$ F=3633.08, df=9, P<0.0001) and the micro-habitat/disturbance level ($r^2=0.723$, F=1604.39, df=50, P<0.0001).

5.16d Bee Hives

The second most dominant use of trees by sun bears in this study was foraging for bee hives, but on its own this food item could not explain much variation in bear signs. Again, general habitat type was an important effect on the distribution of bee hives, particularly relative to bear signs ($r^2=0.510$, F=3569.64, df=9, P<0.0001). In this case, the highest mean frequencies of bee hives were observed in primary lowland forests of East Kalimantan, followed by primary forest swamps, and then older secondary forests. Relative to bear sign frequency, however, bee hives alone could not clarify sufficient variance ($r^2=0.003$, F=99.99 df=1, P<0.0001). With disturbance as an interactive effect the trend remained: the highest mean abundances of bear signs relative to bee hives were in primary lowland forest, followed by primary lowland swamp, and then secondary forest older than 20 years, whereas the lowest observed frequencies of bee hives were in disturbed sites ($r^2=0.7223$, F=1605.40, df=50, P<0.0001).

5.16e Ant Colonies

Although ant foraging was not observed to be as substantial as termites, ant remains were observed in scats and were a frequent food item for sun bears. The overall observed availability of ants in the present study was much higher in disturbed areas than in primary forest ($r^2=0.513$, F=3606.33, df=9, P<0.0001). At alpha-scale resolution, differences were again more significant ($r^2=0.723$, F=1610.46, df=50, P<0.0001), revealing that ant colonies were observed to be most abundant in teak gardens. Although primary lowland forest swamps showed the second highest mean abundance and other primary forest habitats were also highly abundant with ant colonies, disturbed areas such as secondary forests, logging roads, secondary forest swamps, edge forests, orange groves, oil palm plantations, and conventionally logged forests, respectively, were consistently more abundant. Relative to bear sign frequency, ant abundance alone could not clarify sufficient variance ($r^2=0.019$, F=612.87, df=l, P<0.0001).

5.16f Forage Relative Abundance Index

In terms of overall forage diversity, coverage, and abundance, the most variation in bear signs among transects that could be explained by a single biogeographic parameter was the forage Relative Abundance Index (RAI). The index was significantly different across habitat types, where the highest indices were in mid- to upper-elevation primary forests (500 – 1,200 m asl), followed by secondary forests > 22 years, edge forests, primary lowland swamps, and then primary lowland forests, respectively (r^2 =0.588, F=148.93, df=294, P<0.0001). Without the interactive effect of habitat type, the index could not alone explain any variance in bear sign (r^2 =0.006, F=171.91, df=l, P<0.0001). When examined at alphascales across 50 different disturbed and undisturbed habitat types, the interactive effect of disturbance with this index rose significantly, explaining 75% of the error variation in bear signs (r^2 =0.7505, F=750.87, df=50, P<0.0001). Primary undisturbed forests were highly productive. Secondary forests had slightly higher mean abundance indices, but forage diversity was lower and was dominated by significantly fewer forage groups and species.

5.16g Forage in Disturbed vs Undisturbed Sites

When examining the mean abundances of sun bear foods as a whole in disturbed and undisturbed landscapes, a surprising pattern emerged. The mean abundance of primary sun bear foods was significantly higher in disturbed areas *versus* undisturbed sites (table 5.16) ($r^2=0.555$, F=8.99, df=35, P<0.0001). This pattern included most food items individually, as well as when modelled in the forage Relative Abundance Index or when combined as one variable, Total Forage. In general, there was an overall weak negative correlation between total signs and Total Forage because higher abundances of most foods were in disturbed areas avoided by bears. An example of this relationship is seen with fruit, where there were strong negative correlations between bear signs and fruit in areas with very high fruit

abundance, such as in gardens (Pearson's r = -0.717) and edges (Pearson's r = -0.397) that were avoided by bears. Two important exceptions were that mean bee hive and termite colony abundances were higher in undisturbed primary forests than in disturbed areas. As an interaction with Total Forage, disturbed *versus* undisturbed sites were the only significant effect in the model ($r^2=0.565$, F=10.68, df = 35, P=<0.0001).

			1		
	Principal Bear Forage	Mean per Transect	S	Min	Max
	Fruit	6.260	4.25	0	28.0
	Termite Colonies	2.415	1.64	0	10.0
	Ant Colonies	0.588	0.80	0	5.0
Undisturbed	Bee Hives	0.062	0.27	0	2.0
Sites	Mushrooms	0.007	0.09	0	4.0
Sites	Succulants/Tubers	0.040	0.20	0	2.0
	Other Forage	0.087	0.29	0	2.0
	Total Forage	11.468	4.41	2.0	33.0
	Rel. Forage Abundance Index	0.220	0.09	0.1	0.73
	Fruit	6.647	5.08	0	24.0
	Termite Colonies	1.732	1.70	0	9.0
	Ant Colonies	0.815	0.93	0	6.0
Disturbed	Bee Hives	0.058	0.26	0	3.0
Sites	Mushrooms	0.025	0.24	0	4.0
Siles	Succulants/Tubers	0.020	0.14	0	1.0
	Other Forage	0.215	0.43	0	2.0
	Total Forage	11.504	5.56	0	30.0
	Rel. Forage Abundance Index	0.232	0.09	0.1	0.53

Table 5.16. Principal bear forage in disturbed versus undisturbed areas.

5.17 Forest Cover and Refugia

Canopy cover, ground cover, and refugia (escape cover) appeared to be prominent factors in sun bear habitat use. Across sites, regression analyses revealed canopy cover (r^{2} = 0.413) and refugia (r^{2} =0.492) had moderate to strong relationships with sign abundance (figure 5.17). When controlling for habitat type and disturbance at the transect level in a GLM, these variables were significant factors among transects (r^{2} =0.733, F=1622.49, P<0.0001). Areas with the highest frequencies of bear signs were in primary forests, where canopy covers were > 95%, refugia was at least 3.98 on a scale of 0 – 4 (4 being the highest degree of accessible escape cover), and ground cover was < 20%. Although ground cover can be important for security, too much ground cover in the Tropics can negatively affect a larger animal's ability to move through and between habitats, and there was a negative correlation between ground cover (< 35%) and refugia (level < 1 – 2) while higher in ground cover (> 25%). Disturbance was the most significant effect on refugia (r^{2} =0.863, F=81.92, df =21, P<0.0001) and canopy cover (r^{2} =0.805, F=53.57, df =21, P<0.0001).



Figure 5.17. Regression plots of total sign relative to (A) canopy cover and (B) refugia (escape cover) means, averaged at the 1,000 m transect level across sites.

When tested on an individual basis, each variable was highly significant (P<0.0001) across transects where, again, sites with the most bear signs were in primary forests with means of 93% canopy cover, high amounts of refugia ($\bar{x} = 3.6$), and relatively low ground cover < 19%. The second highest frequencies of bear signs were in older secondary forests, where these cover variables more closely resembled undisturbed primary forests that had correspondingly higher frequencies of bear signs ($r^2=0.505$, F=464.2 P<0.0001). Secondary forests had higher canopy and escape covers and lower ground cover than swamps, where bear sign frequencies were lower. Where sign frequencies were lower in primary forests, canopy cover averaged 31.7%, ground cover was > 27%, and escape covers (< 1) with ground cover as high as 100%.

5.18 <u>Topography</u>

Topographic variation can sometimes affect animal movements and habitat selection. This can occur directly by landscape features that either facilitate or limit access to suitable habitats (e.g. steep terrain, canyons, accessible water source) and/or by directly affecting the productivity of habitats through elevation, slope and aspect. Although the general model resulted in significant differences for these parameters among transects (r^2 =0.746, F=851.17, df=60, P<0.0001), differences were most attributed to elevation (F=1753.69, P=<0.0001). Slope, aspect and distance to water sources were not different among transects. Relative to bear signs, general topographic variation had little affect on bear sign abundance (r^2 =0.162, F=396.04, df=15, P<0.0001).



Figure 5.18. Mean sun bear sign frequencies/ha at various elevations across study sites.

When controlling for habitat and disturbance, the interaction of disturbance with elevation accounted for at least 75% of the variation in bear signs ($r^2=0.756$, F=1911.76, df=50, P<0.0001). The highest frequency of signs were also observed in mid-elevation sites between 500 – 1,000 m asl (figure 5.18). These sites were the most remote and furthest distance from major habitat disturbance and human activity, such as logging, villages, agriculture, roads, and consistent hunting/gathering ($r^2=0.783$, F=920.83, df=22, P<0.0001). Figure 5.19 illustrates the differences in the predicted error of total bear sign as affected by topography when tested alone (fig. 5.19A) and when tested with the interactive effect of disturbance (fig. 5.19B).



Figure 5.19. Plot of observed *versus* predicted values of total sign abundance as affected by (A) topographic factors: elevation, slope, and aspect. Little variance was explained other than by elevation. (B) When disturbance interacted with these same topographic variables a much more significant result was found. Note: Regression line in plot (B) added for graphic visual aid.

Chapter 5

5.19 Inter-specific Competition

5.19a Competitor Diversity

Diversity indices of competitor presence/absence data reflected differences among habitat and disturbance types. At least 49 competitors were observed by signs, sightings or calls (table 5.17) and 48 of the 49 observed vertebrate competitors were present in primary forests, which was 68% higher than in the habitat with the next highest competitor diversity (secondary forest > 20 years old). Four of the five main diversity indices in programme PISCES indicated that primary lowland forests were the most diverse and heterogeneous in observed vertebrate competitors, followed by secondary forests > 20 years old and then primary lowland swamps. One index, Simpson's D, suggested that primary lowland swamps (D = 5.588) were slightly more diverse than primary lowland forests (D = 5.394) and these two indices cross in the Rényi measure (fgure 5.20) making them potential uncomparable. At finer scales of geographic resolution, however, primary lowland forests remained the most diverse and heterogeneous overall, followed by mid-elevation primary forests (500 - 750 m)asl), primary lowland swamps, and then secondary forests > 20 years old, respectively. Bootstrap randomisation procedures (Solow 1993) in PISCES demonstrated differences were significant at both the general habitat level and at alpha-scale resolution. Not surprisingly, local gardens and large oil palm plantations were the least heterogeneous and were dominated by a handful of generalist species, particularly Sus spp., Viverridae spp., and Sciuridae spp. The Rényi diversity-ordering index illustrates the competitor diversity differences among general habitat types (figure 5.20).



Figure 5.20. The Rényi diversity ordering index (Rényi, 1961) of sun bear vertebrate competitor diversity among general habitat types.

5.19b Bear and Competitor Overlap:

Like forage, interspecific competition has long been known to influence animal movements, behaviour, habitat selection, health, survival, and fitness. The dominant form of competition between sun bears and other species is likely for food, specifically fruit and termites. A large portion of tropical forest vertebrates on Borneo and Sumatra are frugivores and/or insectivores, with some species filling both niches (MacKinnon *et al.* 1996, Whitten *et al.* 2000).

Table 5.17. Observed sympatric competitors by sign, sightings and calls on Borneo and Sumatra. Note that some genera could not be identified to species level based on sign alone, and some competitors, such as Dhole and domestic dogs, also may be antagonistic species with bears.

Common Name	Scientific Name	Common Name	Scientific Name
Bat (fruit)	Pteropus vanpyrus	Monitor Lizard	Varanus salvator
Bat (fruit)	Pteropus hypomelanus	Moon Rat	Echinosorex gymnurus
Binturong	Arctictis binturong	Mouse Deer (Greater)	Tragulus napu
Buffalo (water)	Bubalis bubalis	Mouse Deer (Lesser)	Tragulus javanicus
Cat (domestic)	Felis domesticus	Muntjac (Yellow)	Muntiacus atherodes
Civet	Viverridae spp.	Muntjac (Red)	Muntiacus muntjac
Dhole	Cuon alpinus	Orang-utan	Pongo pygmaeus
Domestic Dog	Canis familiaris	Otter	Lutra spp.
Eagle (Grey-headed Fish)	Ichtyopharga ichthyaetus	Pangolin	Manis javanica
Elephant	Elephas maximus	Partridge	Rollulus rouloul
Gibbon	Hylobates spp.	Pheasant (Argus)	Argusianus argus
Gibbon	Hylobates muelleri	Pheasant (Bulwer's)	Lophura bulweri
Goat (domestic)	Capra aegagrus	Pig (East-Asian)	Sus scrofa
Hornbill	Buceros spp.	Pig (Bearded)	Sus barbatus
Hornbill (Great)	Buceros bicornis	Porcupine (common)	Hystrix brachyura
Hornbill (Helmeted)	Buceros vigil	Porcupine (Thick-spined)	Thecurus crassispinis
Hornbill (Rhinoceros)	Buceros rhinoceros	Rat	Ratus spp.
Hornbill (Oriental Pied)	Anthracoceros albirotris	Sumatran Rhinoceros	Dicerorphinus sumatrensis
Langur	Presbytis spp.	Sambar	Cervus unicolor
Langur (Hose's)	Presbytis hosei	Serow	Naemorhedus sumatrensis
Langur (Thomas')	Presbytis thomasi	Shrew	<i>Tupaia</i> spp.
Macaque (Long-tailed)	Macaca fascicularis	Siamong	Hylobates syndactylus
Macaque (Pig-tailed)	Macaca nemestrina	Squirrel	Sundascicurus spp.
Marten	Martes flavigula	Tuft-ground Squirrel	Rheithrosiurus macrotis
Mongoose	Herpestes spp.	Unknown spp.	

Odds ratio and chi-square tests were conducted to examine overlap between sun bears and their primary sympatric vertebrate competitors (table 5.18). The chi-square test was significant ($X^2=201.18$, P<0.0001) and the odds ratio was 2.0105 with an associated confidence interval that did not include 1 (tables 5.18 B and C). Hence, the probability that bear presence was dependent on the presence of these competitors can be rejected. In other words, the odds that bear signs were present when competitor signs were present

(4392/21164=0.2075) were 2.01 times higher than when competitor signs were not present (494/4786=0.1036) (table 5.18A). Sign and aging data (or by sightings and calls) from sign surveys showed that both geographic and temporal overlap were extremely common between bears and their most significant competitors (primates, ungulates, civets, pangolins, and frugivorous birds). Tests of positive-matching dichotomy correlation coefficients (S²) revealed 89.9% overlap, and regression analyses suggested competition could not explain variation in bear sign occurrence (r^2 =0.00991). Common attractants like ripe fruit may actually increase the likelihood of overlap between bears and their competitors. Given the bear's aggressive or antagonistic behaviour, these results indicate that competitive exclusion through the presence of sympatric competitors may be an insignificant effect on bear habitat use.

Table 5.18. Sun bear sign overlap with the presence of sympatric vertebrate competitors. Table (A) shows the cross tabs results, which are significant (B) and produced an odds ratio (C) of 2.01 with confidence intervals that do not include 1, indicating the presence of bears is not dependent on the presence of observed competitors.

			Competit	or Sign	
		Frequency Col Pct	Not Present	Present	Total
	Bear Sign	Not Present	4,786 90.64	21,164 82.81	25,950
	C	Present	494 9.36	4,392 17.19	4,886
		Total	5,280	25,556	30,836
(B)				•	<u> </u>
	Sta	tistic	DF	Value	Prob
	Chi-Square		1	201.1812	< 0.0001
Likelihood Ratio Chi-Squar		e 1	224.1868	< 0.0001	
	Continuity Adj. Chi-Square		1	200.5944	< 0.0001
Mantel-Haeszel Chi-Square		1	201.1746	< 0.0001	
	Phi Coefficie	nt		0.0808	
	Contingency	Coefficient		0.0805	
	Cramer's V			0.0805	
(C)					
	Type of S	tudy	Value	95% Con	fidence Limits
Ca	se-Control (C	Odds Ratio)	2.0105	1.8226	2.2179
Co	hort (Col 1 R	isk)	1.8248	1.6714	1.9908
Co	ohort (Col 2 R	ish)	0.9073	0.8973	0.9174

(A)

Chapter 5

5.20 Agonistic Interactions

5.20a Antagonistic Species Diversity

The majority of antagonistic species signs (75%) were observed in primary lowland and mid-elevation forests, where they were 72% more abundant than in the next most diverse habitat (older secondary forests > 20 years old). At least 72% of all predator signs were generated by clouded leopards, followed by tigers at 16% of the total predator signs observed. The east slope of Gunung Leuser National Park had the most antagonistic species signs (60%), followed by the primary lowland forests of Bulungan. No major predator signs or photographs were recorded in local gardens, oil palm plantations, along logging roads, or in CNV-logged sites. Although Gunung Leuser National Park had the most predator signs, diversity indices suggested that the primary lowland forests in East Kalimantan were more diverse and heterogeneous. About 30% more antagonistic species were recorded in the lowland forests of the East Kalimantan sites. Bootstrap randomisation tests in PISCES for all five major diversity indices indicated these differences were significant.

5.20b Bear and Antagonistic Species Overlap

Predation and agonistic interactions are potential influences on sun bears. In addition to niche expansion for arboreal frugivory, it is possible that the evolution of sun bear arboreal behaviour was influenced by the co-evolutionary forces of predation by large felids, such as tigers and leopards. On peninsular Malaysia, Kawanishi (2002) observed one sun bear carcass presumed killed by tigers and two tiger scats containing sun bear remains. At the minimum, tigers and leopards are presumed to be antagonistic when encountering sun bears.

Odds ratio and chi-square tests were conducted to examine overlap between sun bears and possible antagonistic species (table 5.19). In this case, the chi-square test was not significant (X^2 =1.0023, P=0.3168) and the odds ratio test included 1. Further, positive-matching dichotomy correlation coefficient (S²) tests showed only 8.8% overlap between bears and primary antagonistic species. These results suggest that bear sign occurrence was possibly influenced by predator occurrence. There is a small probability (odds ratio: 1.1340) that the location of bear signs may be dependent on the presence of antagonistic species, such that the odds of bear signs occurring where predator signs were present were actually 1.134 times higher than if predator signs were not present.

It is important to note that predators overlapping with bears may be coincidence due to environmental characteristics or cues, such as foods that attract both bears and predators. For example, a food resource like ripe fruit may attract both bears and predator prey (i.e. Chapter 5

pigs, deer), which then attracts the predators. Geographically, both sign and camera data showed that bears occurred in the exact location (within 1 m) of predators. Again, statistically the probability of this occurring was 1.134 times higher than not occurring, but regression analyses indicated that the presence of predator signs could not explain variation in bear signs (r^2 =0.0002). Thus, predators may not be an exclusionary effect, geographically, on bear habitat selection. Temporally, camera data showed little overlap between bears and their most significant natural predator, tigers. Minimum capture periods between bears and tigers at the same site were 3 days apart. Minimum periods between photo captures of bears and clouded leopards were 6:14 hours and for Asiatic golden cat were 30:40 hours.

Elephants are potentially antagonistic when encountering bears. When elephants were added into the antagonist species-bear overlap model, the results were significant $(X^2=7.638, P=0.0057)$ and the confidence interval for the odds ratio did not include 1. Thus, the probability that bear activity was dependent on the presence of antagonistic species when including elephants must be rejected. In this ease, the odds that bear signs will occur in the same location with antagonistic species + elephants were about 80% higher than if antagonistic + elephant sign were not present. Furthermore, regression analyses suggest that very little variation in bear sign occurrence could be explained by the presence of antagonists + elephants (r²=0.0002), which does not appear to be an exclusionary effect, geographically, on sun bear habitat selection.

Tables 5.19. Sun bear sign overlap with the presence of predators. Table (A) shows the cross tabs results, which are insignificant (B) and produced an odds ratio (C) of 1.134 with confidence intervals that include 1, indicating the presence of bears is possibly dependent on the presence of observed predators.

(A)

		Predator	Sign	
	Frequency Col Pct	Not Present	Present	Total
Bear Sign	Not Present	25,584 84.18	366 82.43	25,950
c	Present	4,808 15.82	78 17.57	4,886
	Total	30,392	444	30,836

(B)

Statistic	DF	Value	Prob
Chi-Square	1	1.0023	< 0.3168
Likelihood Ratio Chi-Square	1	0.9748	< 0.3235
Continuity Adj. Chi-Square	1	0.8755	< 0.3494
Mantel-Haeszel Chi-Square	1	1.0023	< 0.3168
Phi Coefficient		0.0057	
Contingency Coefficient		0.0057	
Cramer's V		0.0057	

(C)

Type of Study	Value	95% Confid	ence Limits
Case-Control (Odds Ratio)	1.1340	0.8864	1.4508
Cohort (Col 1 Risk)	1.0019	0.9980	1.0058
Cohort (Col 2 Rish)	0.8835	0.6932	1.1260

5.21 Sun Bear Demographics

Demographic variation in wild Ursidae is difficult to estimate in the best of circumstances, let alone for sun bears that are perhaps one of the most elusive and cryptic members of the bear family. This is particularly true when using indirect sampling methods, such as signs, camera-trapping and genetics. Nevertheless, all measures were used in an excersise to examine potential biogeographic and disturbance influences on sun bear demographic structure and variation. These included direct sightings and photographs, genetics, and signs such as claw mark and paw sizes.

As noted in the genetic results (Chapter 6), analyses from scat and hair samples could only distinguish individuals and could not determine sex, age, or size class. Given we had only one sighting of a wild sun bear in about 14,000 hours across > 1,500 km of surveying, this method was also not useful. Photographic results (Chapter 6) produced some positive gender and size class IDs, but because sun bears are not 100% identifiable with photos, and because body position of the bear could not be controlled relative to camera angles, photo-trapping results were only partially useful. Surprisingly, the best results were generated by the most indirect method, sign surveys, through which we were able to distinguish general age and size classes of the majority of signs.

The most useful measures were claw marks and prints. Not surprisingly, there were no significant differences among sites when testing mean paw sizes, despite controlling for habitat bias in a mixed model (F=1.26, df=33, P=0.162). Variable substrates, sign age, habitat biases (e.g. bark differences among tree species) and individual differences (e.g. open/wide claws *vs.* closed/narrow claws) all affected sign quality, claw and print sizes, and so forth. Thus, all useable signs were classified into four general categories to account for individual variation and to avoid over-confident or spurious estimates. At least 3 claw or track sets per sign were measured where available to account for such differences, and the width between the centres of the first and fith digits were used, rather than edge to edge, to account for substrate, tree species, or other biases. Track or print width at the toes was used as the most consistent measure because paw length is not present on tree claw marks. Means for each set were classified into four general size/age categories as follows:

- a) cub (claw marks/prints < 6 cm width between centre of 1st and 5th digits)
- b) juvenile or small adult (claw marks/prints 6 6.9 cm width between centre of 1st and 5th digits)
- c) medium-sized adult (claw marks/prints 7 8.9 cm width between centre of 1^{st} and 5^{th} digits)

d) large adult (claw marks/prints ≥ 9 cm width between centre of 1st and 5th digits)

Given that the majority of adult Ursidae are sexually dimorphic (including sun bears) with adult males in some cases being at as much as 30 - 50% larger and/or twice as heavy than females, it is assumed that substantially larger, deeper, and heavier laid claw marks/prints were made by males (e.g. > 11 - 12 cm between centre of 1st and 5th digits). Results showed that about 99% of all observed bear signs were generated by sun bears and could not be confused with any other species. At least 75% of these were successfully classified into respective size/age classes, among which significant differences were found in Kruskal-Wallis tests (X²=755.82, df=8, P<0.0001).

Transects were tested as a random effect in a mixed ANOVA model, which resulted in significant differences among transects (table 5.20). When controlling for the fixed-effects of general habitat classification, there were no significant differences in size classes (F=1.68, df=6, P<0.223) and, as a random effect, general habitat differences were again insignificant. Fourteen biogeographic and topographic variables (e.g. canopy cover, ground cover, slope, aspect, elevation, forage, etc.) were then tested regardless of habitat classification in a logistic model with stepwise regression and the only variables showing effects on bear size class were: canopy cover, ground cover, slope, and bee hive abundance (P<0.036). This result remained unchanged with the addition of competitive and antagonistic species presence in the model.

When general habitat classifications were modelled with all topographic and biogeographic parameters, canopy cover (P<0.0001), bee hive abundance (P=0.029), and habitat type (P=0.0053) were the only significant effects on bear size class variance (X^2 =130.38, df=29, P<0.0001). Finally, disturbance was added as an interactive effect in the model with biogeographic parameters across sites. The only significant effect on bear size class in this final model was disturbance (X^2 =45.64, df=31, P=0.0437), particularly when modelled together with site effects (X^2 =244.31 df=68, P<0.0001). A mixed ANOVA model showed that the most significant effect on bear size class variance was again disturbance among sites (F=10.86, df=15, P<0.0001). Logistic regression of size classes also resulted in significant differences among sites (X^2 =196.99, df=14, P<0.0001) and disturbances (X^2 =9.33, df=36, P<0.0001).

It is possible that small older sign and large younger sign in the same site could be generated by the same bear as it grows. Smaller older sign could also reflect habitat bias, where perhaps bark has grown around large claw marks. In either case, when controlling for sign age in a logistic regression model, the age of signs was not a significant effect on size class (X^2 =1.742, df=l, P=0.1869). This same result occurred when controlling for general habitat differences ($X^2=2.6198$, df=1, P=0.1055).

Not surprisingly, the most prevalent size class was medium sized bears, with claw marks or prints ranging between 7.0 - 8.9 cm wide between the centres of the first and fifth digits. The largest bears were located in primary lowland and mid-elevation forests < 750 m asl, with claw marks as large as 14.5 cm and a mean of 7.81cm. Smaller size classes (mean: 6.84 cm) were found to be more prevalent in disturbed habitats and secondary forests. The largest mean set of claw marks (14.5 cm) and presumably the largest bear leaving sign in this study was observed in primary lowland forest at 405 m asl in the West Bulungan region.

Tables 5.20. Sun bear claw mark and print variation among transects. The upper table provides the covariance estimates, for which the confidence intervals do not include 1. The lower table provides the various Log-Likelihood statistics for best model fit.

	Covariance Parameter Estimates			nates
Cov Parm	Estimate	Alpha	CI Lower	CI Upper
TRANSECT	0.1521	0.05	0.1117	0.2193
Residual	1.7897	0.05	1.7189	1.8650

Fit Statistics	
-2 Res Log Likeliehood	16896.5
AIC (smaller is better)	16900.5
AICC (smaller is better)	16900.5
BIC (smaller is better)	16907.8

Primary forests had more diverse and abundant age and size classes. In contrast, disturbed areas and small forest patches had dense and more homogeneous size classes, and the signs were most often of similar age and apparent origin, suggesting relatively few bears with concentrated activity. For example, in many sites we observed signs clearly made by specific bears, such as the same missing claw on the same digit in every sign; marks of a particular digit shaped in a consistently irregular fashion (e.g. bent in the opposite direction of other claws); or signs made by an adult and cub consistently together and of the same age (i.e. a presumed female with cub). In these cases, we were able to infer that most of the signs were generated by only one or two individuals in that study site.

Bootstrap randomisation tests (Solow 1993) of size class diversity using the five main diversity indices (Shannon-Wiener *H*, Simpson's *D*, Margelef *D*, Berger-Parker Dominance, and Fisher's Alpha) in PISCES showed that the most diverse and heterogeneous size classes of sun bears were observed in primary lowland and lower montane forests < 1,200 m asl. The next highest size class diversity was located in secondary forests older than 20 years. Between Sumatra and Borneo, sites in East Kalimantan were found to have the most diverse and heterogeneous size classes. Although an occasional large claw mark was found in edge forest, these were in primary forest ecotones and were generally outliers with much lower means. It was observed in the field that some of these outliers were due to habitat bias, such as anomalous tree bark effects and/or environmental effects due to more exposure and weathering at ecotones and edges.

Kayan Mentarang National Park on Borneo had the highest diversity and most heterogeneous size classes of all study sites, followed by the Bulungan ecosystem and then Gunung Leuser National Park in North Sumatra. Among all study sites, primary forests in the Jalungkereng area of Kayan Mentarang National Park had the most diverse size classes followed by primary forests in the East Bulungan area. Jalungkereng bears were on average smaller than bears further interior in the Ulu Nnggeng region. In Sumatra, the greatest diversity of size classes were found in the two most remote and undisturbed areas surveyed in that region, Tankahan and Sei Badak respectively, in Gunung Leuser National Park.

Overall results suggest that the largest bears and most diverse size/age classes were observed in remote primary lowland and mid-elevation forests < 750 m asl. If the assumption is valid that claw marks and prints are relatively correlated with bear size and, in some instances gender, results possibly suggest that the most demographically diverse populations would have also been found in primary lowland and mid-elevation forests, but given this assumption is untested, this latter conclusion should be viewed with caution.

5.22 Human Activity

The strongest effects of non-habitat disturbing human presence on bear habitat use were related to the distance and intensity of human activities relative to where and when bears were active. Observed human activities included: (1) general wildlife hunting for protein; (2) non-timber forest product gathering (e.g. damar, bird nests, aromatic woods ('gaharu'), fruit, plants); (3) timber cruising; (4) noise from wood cutting by chainsaw or axe; (5) hunting; (6) transit by walking, boat, bike, jeep, and so on; (7) vehicle traffic; and (8) research. The basic GLM best illustrates this relationship. At the 10 m sub-section level, distance effects examined in isolation were highly significant, but very little variance in total bear signs was explained (r²=0.096, F=3124.24, df=l, P<0.0001). When adding the intensity level of human activities (e.g. average number of people passing along a trail or hunting/gathering in a particular area per month), explained bear sign variance tripled (r²=0.283, F=2311.010 df=5, P<0.0001). This relationship was most significant once human activity levels increased; in this example, from low to moderate numbers of >25 people/month in the area. If examined by human trail use relative to bear use of trails in the same primary forest areas, game trails had a 49% higher mean of 42.9 bear signs/ha, while human trails had 21.9 bear signs/ha.



Figure 5.21. Plot of observed *versus* predicted values of total sign abundance as affected by human activity distance, intensity, type, and timing. There is a strong relationship between the frequency of signs and distance from human activities, particularly as intensity increased from low to moderate levels. Note: Regression line is added for graphic visual aid.

There was a positive correlation in sign abundance when humans were farther away from bear activity (Pearson' s r = 0.311). When testing the type of human activity (n=60 types) along with distance and intensity in a GLM, over 65% of the variation in total bear sign was explained (r^2 =0.652, F=851.37, df=64, P<0.0001). This was most significant once human activity levels increased to persistent numbers greater than 25 people/month. A robust and highly-significant relationship resulted (figure 5.21) once the type, intensity, timing, and distance of human activities were tested in the model as interactive effects on the location and amount of bear signs (r^2 =0.771, F=676.0, df=144, P<0.0001), where > 81% of sites with human activity were avoided. Adding habitat disturbance to the model increased explained variance to 85% (r^2 =0.852, F=858.39, df=194, P<0.0001) and rendered the timing and distance of human activity insignificant.

5.22a <u>Hunting</u>

Hunting surveys were conducted in local villages in all major study areas. Due to the limited number of village leaders (Bupati), these individuals along with traditional knowledge holders (Kepala Adat), village elders, and police were surveyed systematically while the more numerous hunters, gatherers, and the general public were surveyed randomly. Prior to introducing the survey, I found in all sites that extensive social engagement was first required, involving sharing coffee/tea and meals along with exchanges about social/cultural situations of each other. Once these social exchanges progressed to subjects about the environment, the standarised questionnaire with the 5-point Likert scale could be initiated regarding hunting, wildlife and forest ecology. As noted in section 5.6j, the written questionnaire was not accepted in all cases. Thus, to achieve standardisation across sites, all questionnaires were posed verbally and results should be considered accordingly.

In all study sites local people were cautious when divulging details, particularly regarding illegal activities like poaching ("hunting") of protected species. Even though all field assistants were employed from some of the same local villages examined in these social surveys, in the majority of cases (> 63%) confidence was not garnered from the general village populace until we had been working in the area for a minimum of 6 - 12 months, at which point information was openly provided.

In general, survey participants with the longest and most intensive experience in the forest were those with the most knowledge of wildlife and forest ecology. In most cases (>96%) these were men who were regular hunter/gatherers from childhood. Because there is just one bear species that cannot be misidentified as any other animal in Indonesia, there was no confusion about bear hunting or captures. The biggest challenge for these surveys was

trust. Once a positive relationship was established with these men, information on hunting, species killed, locations, and so on was freely offered.

It is important to note that a very broad array of species are hunted for subsistence in Indonesia, particularly in East Kalimantan, and it is unknown how this affects sun bears, including the taking of primary sun bear competitors (e.g. ungulates) and antagonistic species like tigers and clouded leopards. More extensive research is required to address this question. Thus, results reported here are focused only on sun bears, where "take" refers to kills as well as capture and removal of live adults and cubs from wild populations.

Consistent records among sites dated back to 1997. Survey results showed that in three villages of the upper Bahau region (Long Alango, Long Tebulu, Long Punjungan) adjacent to the eastern border of Kayan Mentarang National Park, an average of about 12 bears/year/village were taken on average between 1997 – 2003. In the Bulungan Research Forest, a mean of 6.6 bears/year/village were taken during the same period by villagers in Long Loreh, Long Seturan, and Long Setulang. In North Sumatra and Aceh, an average of > 21.3 bears/year/village were taken by hunters during this same period in the Aras Napal, Tankahan, Ketambe, and Kutacane areas bordering Gunung Leuser National Park. The majority of bears in the latter areas were taken in the Aras Napal and Ketambe regions.

In each area, hunter effort remained stable or increased, but hunter take of sun bears decreased over time (figure 5.22). Statistically, inter-annual take rates were not significant (P > 0.05) by either ANOVA or Kruskal-Wallis tests, but the differences in all areas between 1997 and 2003 were dramatic with a strong declining trend over time. Hunters surveyed in every region stated this pattern was due to fewer bears in the hunters' traditional hunting grounds. Accordingly, it was reported that hunters needed to increase their effort and travel longer and to more remote areas (primarily in protected areas) each year to trap or kill bears.



Figure 5.22. Plot of mean number of bears taken/year by region. Annual rates in each region were not statistically different, but there is a strong declining trend.

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It was reported by interviewees that the majority of bears taken among villages during this period were from protected areas because interviewees found bear populations outside of these parks were too diminished to justify their effort and expense.

5.22b Bear Physical Condition

The physical condition of bears taken at these sites during 1997 - 2003 was reported to be good to excellent. There were no reports of bears with disease, malnutrition, or unhealthy condition during this period. All interviewees stated that bears were healthy, had moderate to high sub-coetaneous and bone-marrow fats and lustrous coats without signs of mange or abnormal condition. Bear meat and organs were reported normal in all cases and had typical taste, consistency, and odour.

5.22c Uses of Bears Taken

The primary uses of bears taken were the same in all areas. The most dominant use was body parts sold for traditional medicinal use (i.e. gall bladders and derivatives) followed by cubs for sale as pets. In the interior Dayak villages of East Kalimantan, gall bladders sold locally for as little as \$2 USD, whereas they were more than four times that amount in North Sumatra. Bear cubs were selling at an average rate of \$100/cub in Sumatra, with a range from \$10 – \$500. In East Kalimantun, bear cub sales were not as prevalent as in Sumatra and averaged less than \$50/cub, ranging below \$10/cub and as high as about \$250. Claws were an important use for traditional ornaments in most areas, selling in Sumatra for about \$2 – 5/claw and \$1 - 2/claw in remote areas of East Kalimantan. In 2003, teeth of both bears and clouded leopards were still prized in East Kalimantan for traditional Dayak ornamentation, more so than in Sumatra, but because supplies from wild or captured bears were low in all areas, plastic replicas were becoming more prominent. Due to apparent declining bear and clouded leopard populations in the Malinau district of East Kalimantan, the Long Loreh village head imposed an informal policy in 2003 that the taking or killing of bears and leopards was no longer allowed.

Gall bladders in interior East Kalimantan were mainly sold and used locally, but in Sumatra sales to larger or regional markets were more common. This was primarily due to easier access in Sumatra to such markets *versus* much lower/no access from the interior forests in East Kalimantan. East Kalimantan interviewees reported that increased access *via* the proposed trans-Bornean highway from Malinau to the upper Bahau region would increase their motivation to hunt and sell more wildlife, wildlife by-products, and other forest products and would add pressure on wildlife and other natural resources in the region. CHAPTER 6

SUN BEAR DENSITY AND ABUNDANCE



SITE OCCUPANCY AND HABITAT USE

METHODS

The overall objectives of this phase of research were to examine sun bear site occupancies, densities, and distributions *via* genetic sampling, camera trapping, and sign surveys. Genetic sample mark-recapture methods were conducted throughout the study in conjunction with sign surveys and camera trapping from 3 September 2001 to 5 May 2004 and camera-trapping methods from 11 November 2001 to 5 May 2004. All camera-trapping and genetic surveys were conducted in the same study sites as sign surveys. Integrating sign surveys with site-occupancy and density estimates produced more reliable predictions of sun bear habitat use and distributions. This method redundancy and geographic overlap also provided correlative data regarding the **(a)** efficacy of these methods and **(b)** estimated density and abundance of bears potentially generating signs.

Objective 2: Sun Bear Densities and Distributions

To address the assumptions that biogeographic condition, habitat disturbance, and human activity affect sun bear habitat, resource, and landscape uses, density estimates were needed for more reliable predictions of the potential number of bears using various habitat types in disturbed and undisturbed conditions. Determining the spatial distribution and density of an elusive and cryptic species like the sun bear is difficult and capture success rates by other studies to mark and radio collar sun bears have been very low by conventional trap-and-release techniques (Fredriksson 2001, Wong 2002). Thus, other methods were employed. Sign surveys in this study provided data on the relative distributions, as well as habitat, resource, and landscape uses by sun bears, but that method alone did not enable bear density estimates. Thus, site-occupancy and capture-recapture methods were used.

Collection of genetic samples occurred during sign censues, camera trapping, and opportunistically throughout the study. A system of automatic 35-mm cameras fitted with active infrared sensors were located *via* a stratified-random study design in the same grids and sites as sign transects and genetic sampling. Resulting camera data were analysed separately and relative to sign data and genetic mark-recapture data from the same areas. This stratified-random correspondence by site among camera traps, sign surveys, and genetic sampling, rather than fully random locations, provided strong redundancy, robust presence-absence and site-occupancy data, and some bear identities. Integrating these methods provided a robust means to estimate site occupancies and potential sub-population densities, abundances, and distributions relative to the density and frequency of signs for each site.

6.1 Genetic Mark-Recapture Study

The primary objective for genetic analyses was to generate individual and sex identification based on scat and hair samples collected by sign surveys and opportunistically. All samples were sent to an independent laboratory every 3 - 6 months to stabilise the DNA through extraction procedures. Dr Lisette Waits of the Fisheries and Wildlife Department Genetics Laboratory at the University of Idaho, who is analysing sun bear scat and hair samples from other parts of its range, conducted the analyses (Waits 2004).

Microsatellite amplification and mitochondrial sequencing methods (Waits 1996, Craighead and Vyse 1996, Waits *et al.* 1999) were conducted on hair and scat samples from different habitat types in disturbed and undisturbed areas to generate gene flow estimates and relatedness. This was intended to serve as a mark-recapture method to (a) help distinguish individual bears, (b) estimate genetic variability, (c) refine population density estimates through "recapture" procedures, and (d) facilitate more precise assessments of sign survey and camera-trapping data. The latter included identifying individual bears, the locations and distances between samples and, thereby, possible home ranges, overlap, and bear use of the overall landscape matrix. Glucocorticoid hormone levels, which materialise in scat *via* stress responses and persist as faecal metabolites, were intended to be analysed in scats from disturbed and undisturbed sites to measure the physiological impacts from disturbance (Hunt *et al.* 1999, Waser *et al.* 2004), but samples were not good enough for such analyses.

Mark-recapture genetic sampling has proved effective on very large, remote and rugged landscape scales, including in North America for grizzly bears (Kendall 1999, Kendall *et al.* 2001) and American black bears (Servheen *et al.* 1999). Hair-snagging techniques were initially tested on wild sun bears by G. Fredriksson in Sungai Wain Protection Forest, East Kalimantan but, because sun bear hair is very short and strong, this method could not provide enough roots and follicles for appropriate genetic samples. (Augeri 1999, G. Fredriksson pers. comm.). Trained scat-detecting dogs were initially part of this sampling design, but permits were not approved. It was necessary, therefore, to survey for samples during sign transect and camera-trapping surveys as well as opportunistically.

GPS coordinates were recorded for all scat and hair sample locations. Sterilised surgical gloves and tweezers (for hair samples) were used for collecting samples in order to avoid sex ID contamination and cross contamination of samples (L.P. Waits pers. comm.). For hair, only those samples that contained both the hair and the root follicle were used. All hair samples were preserved in labelled paper envelopes made by a female assistant to minimise sex ID contamination by males, and were then placed in zip-lock bags with indicating silica beads.

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Scat samples were collected in plastic bags and preserved, a portion of which were stored in 96% ethanol for genetic analyses. According to the most current protocols, 10 - 15 ml of ethanol to 2 - 3 ml scat was described as the best ratio for DNA extraction (Murphy *et al.* 2001). Because scats are not uniform in contents, each scat was mixed in place as much as possible to attain a homogenised sub-sample for both genetic and diet tests (L.P. Waits pers. comm.). A twig from a local tree that was too small to support animals, thereby minimizing species contamination was used to mix the scat sample in place. After mixing, the same twig was used to place 2 - 3 ml of different portions of the scat in a sample tube with 10 - 15 ml of ethanol. Because refrigeration was not available in the field, samples

of these study areas, the average time period before shipping samples was 3 - 6 months.

were stored at ambient temperature until they could be shipped. Due to the remote locations

6.1a Micro-Satellite Amplification and Mitochondrial Sequencing

Objectives for micro-satellite amplification and mitochondrial sequencing were to:

- (1) determine the identification of unique bears from each genetic sample and
- (2) determine the mitochondrial DNA haplotype of each sample and compare for matches.

Samples were analysed by Dr Lisette Waits in the Genetics Laboratory of the Fisheries and Wildlife Department at the University of Idaho. Following is a description of the procedures from the laboratory (Waits 2004). All DNA extraction and PCR set-up were performed in a low-quantity DNA room that was dedicated to processing bone, scat, and hair samples to avoid contamination errors (Taberlet *et al.* 1999). DNA was extracted using a Qiagen Tissue Kit or Qiagen Scat Kit (Qiagen Inc., Santa Cruz, CA.).

Individual identification: Individual identification normally uses a suite of six or seven microsatellite loci of 220 base pairs or less (ABCLMPJ) (Paetkau and Strobeck 1994, 1997, Paetkau *et al.* 1998). Black bears have been previously surveyed across North America using six of these loci (ABCLMP) (Paetkau and Strobeck 1994, 1997, Paetkau *et al.* 1998) and a large number of alleles (2 - 14) have been identified. All 7 loci (ABCLMPJ) have also been used extensively in brown bear populations and a large number of alleles (3 - 12) have been identified (Paetkau, *et al.* 1998). Polymerase chain reaction (PCR) conditions and ABI gel separation methods are described in Woods *et al.* (1999). Genotypes for each sample were determined using the Genescan and Genotyper software packages (Perkin Elmer).

Samples were originally tested using a duplicated BL PCR duplex. Samples that showed any sign of success with the BL duplex were re-PCRed using B, L, and AC. Success rates did not improve for B or L and the AC duplex also had very low success rates (1 A and 4 C). Thus, the samples were re-run using the A and C PCRs duplicated.

Mitochondrial DNA Sequencing: Sequences were obtained using a long fragment of the gene L16345 and H16751 (Ward *et al.* 1991). Samples that failed with the long fragment were re-attempted with either the newly-developed Carnivore primers (~120 base pairs, Waits unpublished) or the Farrell *et al.* (2000) primers (~150 base pairs). The PCR products were purified using an exo-sap enzyme method. Using the purified PCR products for a template, cycle sequencing reactions were prepared using the Big Dye Terminator Ready Reaction Kit (PE Applied Biosystems) following a modified version of the manufacturer's protocol. Unincorporated primers and dye-terminators were removed using sephidex spin columns. Sequence reactions were loaded in a 5% long ranger (BW Products) denaturing gel on an ABI prism 377XL automated sequencer (PE Biosystems). The resulting sequence was analysed using Sequence Analysis (ABI) and Sequencher 3.1.1 (Gene Codes Corp.), comparing sequence fragments, correcting base-calling errors and verifying polymorphic sites. Results were then blasted in Genbank to verify species.

6.2 <u>Camera-Trapping Surveys</u>

Karanth (1995), Karanth and Nichols (1998), Carbone et al. (2001), and O'Brien et al. (2003) demonstrated methods with theoretical foundations in capture-recapture sampling studies that estimate the densities of cryptic animals like tigers using cameras and the software programme CAPTURE. Carbone et al. (2001) examined the camera-trapping capture rates from 19 tiger studies across the species' range and found the number of camera days for each tiger photograph possibly correlates with independent estimates of tiger density. O'Brien et al. (2003) and Kawanishi (2002) used capture rate indices in their respective studies for relative abundance estimates. The three latter studies suggest that estimates do not need individual animal identity. But results from the current study indicate there are associated problems with these methods, which were not useful in my study sites for estimating population densities for species that are not individually identifiable. Detection and site-occupancy models developed by MacKenzie et al. (2002, 2003) apply capture-recapture principles at the site and species level in probabilistic arguments, but do not require individual animal identifications, are based on rigorous detection - non-detection data, and are more statistically and theoretically robust. Considering that sun bears are cryptic and elusive and that the probability of identifying individuals is much lower than for tigers, presence-absence and site-occupancy methods (MacKenzie et al. 2002, 2003, Royle and Nichols 2003, Hines 2004) were applied in this portion of the current study.

In addition to site-occupancy, detection-probability, density, and distribution estimates, valuable information was generated on sun bear habitat use and activity times, which were analysed relative to biogeographic conditions, disturbances and human activities. Given the diversity of habitat types, environmental conditions, and so forth across the species range, density estimates beyond this study may not be accurate. Thus, density estimates were only generated for those sites examined in this study in Indonesia.

There is no set minimum or maximum sampling area for camera studies. The most important factor is the ecology of the species, but the final sample area size is tempered by logistics, personnel, and funding. Carbone *et al.* (2001) showed that the sample areas for tiger camera studies in South-East Asia (including in Gunung Leuser National Park and three other Sumatran National Parks) ranged from 83.3 to 836 km², with an average of 261.9 km². The sample area for O'Brien *et al.* (2003) in southern Sumatra was 20 km² whereas Karanth and Nichols' (1998) four tiger sample areas varied between 121.6 – 282 km². Considering that the sun bear has a smaller home range (4 – 20.6 km²) (Meijaard *et al.* 2005) than tigers, and the current study was conducted entirely on foot in very remote areas (as opposed to many other camera-trapping studies that are conducted by vehicle along jeep tracks and

roads), sample areas of 64 km²/study site were used in Sumatra and 48 km²/study site were used in East Kalimantan, which provided suitable coverage for ca. 2 - 4+ bears/site.

For trap density, Karanth and Nichols (2000) suggested a rough guide of 1 - 2camera traps/tiger home range based on those tigers with the smallest home range (usually adult breeding females at $\approx 15 \text{ km}^2$). Published quantified home range data for sun bears in Sabah via VHF telemetry are $6.2 - 20.6 \text{ km}^2$, with mean of 14.8 km² (± 6.1 SD) (Wong 2002). Meijaard *et al.* (2005) note that the sun bear's home range on Borneo is $4 - 20.6 \text{ km}^2$. Example average annual adult home ranges for the sun bear's closest kin (Ursus thibetanus and U. americanus) are: males = 66.06 km^2 and females = 26.37 km^2 for Ursus thibetanus in Japan (Servheen *et al.* 1999) and for *U. americanus* males = 44.1 km^2 and females = 16.9km² in South-Eastern U.S. (Powell et al. 1997). Female home ranges are ca. 2 – 3 times smaller than males in most Ursids and other large mammals. It is also certain that bear home ranges vary with forage availability over seasons and years as well as with the extent of suitable available habitat (Jonkel and Cowan 1970, Rogers 1976, 1987, Craighead et al. 1995, Powell et al. 1997). This is particularly true in the Tropics with asynchronous and aseasonal fruiting and patchy forage distribution. Thus, given mean home ranges of sun bears (14.8 km²) and its closest Ursid female kin and female tigers, 2 trap sites/4 km² was used to maximise trap density (Karanth and Nichols 2000) at 8 traps/16 km².

Depending on the focal area and map availability, a 1 or 2 km² grid was overlaid on the same stratified-random study areas as sign and genetic surveys on 1:50,000 or 1:100,000 topographic maps and, where available, habitat classification maps from existing GIS data layers and the latest TM 10 m panchrome data from Landsat 7. A representative sample of habitat and disturbance types, including areas with and without hunting, with varying topographic and biogeographic features were randomly selected for each camera site for comparison. A stratified-random sample of survey sites was selected in each focal area, such that six 64 km² sites in Sumatra and four 48 km² sites in East Kalimantan were delineated.

For example, a 64 km² block of forest was stratified by say, primary forest, randomly delineated, surveyed, and compared with another survey in an adjacent 64 km² block of secondary forest in the same ecosystem with similar biogeographic conditions. Within each survey block, specific sub-habitat (e.g. lowland, montane, swamp), topographic (e.g. elevation gradients), and disturbance (e.g. conventional logging, hunting, etc.) features were sampled as fixed effects within the grid cells and compared among surveys. Camera trap locations were selected randomly (described below) and spaced systematically at 2 trap sites/4 km², enabling 32 camera-trap stations/study site in Sumatra (n=6 study sites) and 24 trap stations/study site in East Kalimantan (n=4 study sites). All traps were spaced a

minimum of 1-2 km apart. A total of 280 camera-trap stations were used across the 10 study areas. Surveys were conducted simultaneously on Sumatra and Borneo by multiple teams.

Other camera studies suggest maximising capture success by selectively placing traps only in locations assumed to be predominantly used by the focal species, especially along trails and roads, which are assumed to be used more often than off trail/roads and provide easier access for researchers. However, these strategies increase biases in geography (i.e. limited strata, e.g. trapping only along trails/roads and/or in assumed preferred habitat), abundance and distribution (i.e. assumed higher use of trails/roads or particular sites), trapsite selection (i.e. trap-selection bias by workers, e.g. easiest access along trails/roads), and may violate the assumption of equal access to all traps for particular species (i.e. individuals in ranges without trails/roads or in assumed non-preferred habitat may not be observed). Such biases must be weighed against maximising capture success. Current and previous sign surveys (Augeri 1999, 2000, 2001, 2003) showed that sun bears do not bias activity more to trails or roads like that observed in territorial carnivores in other studies (*see* Griffiths and van Schaik 1993, Karanth and Nichols 1998). Results revealed significantly higher sun bear sign frequencies off human trails/roads and 49% higher use of game trails than human trails.

Thus, camera trap locations within every 4 km² cell were randomly located regardless of biogeographic condition by applying a stratified-random design. Randomly numbered quadrants in every grid for each habitat and disturbance type were selected using a random numbers table and then pre-surveyed for possible camera-trap sites during sign censuses using random compass bearings according to a random numbers table. Random grids were then selected and pre-surveyed in the same manner again over 2 - 3 week periods directly prior to camera trapping. Trap sites may have included trails only by chance according to random locations and compass bearings. Data from sign, habitat, and genetic surveys were used to help locate suitable camera sites in the field in coinciding grids. Random sites in grids with positive signs of sun bear activity were used for those trap sites. In grids with no sign, trap sites were located according to randomly selected map coordinates for that grid and then in the field according to the best assumed capture success, e.g. at termite colonies or fruiting areas, along game trails, etc. Baiting was not used to avoid trap selection bias by bears. This method improved camera-trap locations by using a randomised design plus verified sun bear activity, including locating random trap sites during random periods in random areas with and without sun bear sign according to the best assumed capture success.

TM1500 Trailmaster active-infrared automatic 35-mm camera systems (Goodson & Associates, Inc.) were positioned at the two randomly located trap sites within each 4 km^2

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grid cell. In the Sumatran study sites, this research was conducted in collaboration with the Leuser Management Unit, which generously provided field assistants, cameras, and film with the dual goal of studying the densities and distributions of the Sumatran tiger (Panthera *tigris sumatrae*) and sun bear. Capture – recapture identification methods for tigers were based on unique stripe patterns and required dual-camera systems for photographs of both sides of the animal. Thus, dual camera systems were set-up at 50% of the Sumatran study sites to accommodate tiger identification. Where possible, individual bears were identified based on size, chest crests, pelage, gender, body markings, and so forth. At all non-dual camera sites, single cameras were oriented at a 45° angle to the focal point for maximum ID potential. Logs, stones, and other hardened forest materials were placed directly below the infra-red beam in a natural setting to (a) slow animals to improve photographic quality and increase photo captures and (b) oblige bears to raise their bodies, thereby exposing their chest-crests for possible identification. The width between the active infra-red transmitter and receiver ranged ca. 3-5 m wide. Brush and other debris were placed in a natural setting along the edges of the trapping "path" from the infra-red beam to > 20 - 30 + m along both sides of the trapping path to direct animals to the trap site. All camera cables were wrapped in duct tape to protect against termite, ant, and other animal damage. The entire trap system was cleaned with alcohol to remove human scent and camouflaged and protected with brush.

Karanth and Nichols (1998) reported that 2 - 3 month trapping periods were sufficient for coverage of tigers moving in their range and were brief enough that mortality, permanent/transient movement in and out of the study areas, and other violations of closure assumptions were minimal. In the current study, all cameras operated 24 hr/day x 8-10 weeks in Sumatra and 24 hr/day x 7-8 weeks in East Kalimantan. The interval between photos was 0.6 seconds. Once surveys ended, cameras were rotated to another sampling area until at least two sites were sampled in each focal area (Karanth and Nichols 1998). To coincide with seasonal shifts in food availability and bear behaviour, random periods during both wet and dry seasons were sampled over multiple years in Sumatra (2001 – 2004) and across both seasons in East Kalimantan (March – November 2003). Each camera station was checked, shut down, cleaned/repaired, and film changed as needed every 5 - 7 days. Sampling effort was defined as the sum of all nights that traps functioned and capture history matrices (Wilson *et al.* 1996, Karanth and Nichols 1998) were created for all trapped species.

Although photo identification rates for sun bears were as high as 70% in East Kalimantan, 100% identification is required for traditional capture-recapture models. A beneficial aspect of presence-absence models is that they do not require identification of individual animals. This method is more statistically and theoretically rigorous than capture

rate methods proposed by Carbone *et al.* (2001), Kawanishi (2002), and O'Brien *et al.* (2003). Thus, all data for the present analyses were analysed as verifiable presence-absence data and were modelled in the software programme PRESENCE version 2.05 (Hines 2004) according to models developed by MacKenzie *et al.* (2002) and Royle and Nichols (2003). Because detection probabilities are contingent on animals being present and available for detection (Royle and Nichols 2003), presence or absence needs to be accurately recorded and camera trapping was an excellent method for validating presence data from sign surveys.

For camera-trapping as presence-absence (detection – non-detection) data, model precision was best assured by identifying photo captures as independent photo events (i.e. distinct sightings) verifying species presence. Obvious consecutive triggering of a camera at the same site producing multiple photos of the same animal was considered one photo event. This is an important distinction with other studies that use capture rate as an index of animal abundance (Carbone *et al.* 2001, O'Brien *et al.* 2003, Kawanishi 2002). While the latter is based on probabilistic arguments, all individuals should be identified--especially for multiple photos and/or "recaptures". Otherwise, it is doubtful if the same/different animals produced the photos. This problem and its assumptions are avoided in site-occupancy methods.

A critical element for camera-trapping survey analyses as presence-absence data is defining the sampling occasion. The optimal method of camera-trapping requires continuous camera operation at different trap sites within the survey area. In this study, every trap site was analysed as a different survey "plot" within the study area. Every 5 - 7 days, each site and camera were checked and film changed, etc. as needed. Traps were then restarted to survey their plots for another 5 - 7 days continually for 24 hr/day. Thus, the survey periods between checks were measured as repeated weekly sampling occasions/plot. This design produced 7 - 9 sampling occasions/plot, with 24 plots/site in East Kalimantan and 32 plots/site in Sumatra. This design aligns well with the MacKenzie *et al.* (2002) model that requires > 5 sample occasions/plot at multiple plots in a survey site to increase model accuracy (MacKenzie *et al.* 2002, Royle and Nichols 2003). The advantages of this design enabled modelling data as detection–non-detection data without individual identifications and produced robust detection probabilities (*p*) and site-occupancy rates (ψ).

6.2a Assumptions

This presence-absence method applies certain capture-recapture principles in probabilistic models and one of the most important assumptions for capture-recapture modelling is that the study areas are ecologically "closed" to individuals (Rextad and Burnham 1991, Wilson *et al.* 1996). Violations include transient, dead, or emigrating

animals in the study area. These individuals would not be captured on multiple occasions and their capture histories would exhibit trap-shy behaviour (Karanth and Nichols 1998).

Potential closure violations were addressed by (1) maintaining the best proven survey period for large carnivores of 8 - 10 weeks, (2) a randomised sub-sample plot design to survey multiple sites in multiple areas at random times across seasons/years, and (3) using camera-trapping results as detection – non-detection data, for which the model employed is only closed at the species level and allows for transient/dead/emigrating animals (MacKenzie *et al.* 2002). Presence-absence model assumptions are noted in Chapter 5, sections 5.2 - 5.3.

All individuals in a sample area should have an equal chance of being photographed independently with equal trapping effort across all sites. This assumption was addressed by (1) spatially- and temporally-random sampling for all trapping periods and locations, (2) trap sites were not stratagraphically limited, were randomly located across all surveyed habitat types and biogeographic conditions, and were sufficiently spaced ($\geq 1-2$ km) and independent given known sun bear home ranges, and (3) consistent trap density in all survey sites and all traps/site operated the same duration; thus, equal trapping effort was attained. A possible limitation is that surveys in Sumatra were on average 5 – 7 days longer than in Kalimantan.

A limitation of capture-recapture methods is that 100% of captured individuals are identified and there is some inference, especially for species that cannot be identified 100% of the time. Violation of this assumption was avoided by analysing data in presence-absence models, which do not require individual identification (MacKenzie *et al.* (2002).

Objective 3: Biogeographic Analyses of Disturbance Effects

6.3 Site Occupancy and Habitat Use

Site-occupancy probabilities for each site were examined *via* **1**) camera-trapping and **2**) sign surveys. For occupancy modelling by sign surveys, the randomly-located 10 x 1,000 m transects were survey "plots" in a study area and 100 - 500 m sub-sections were modelled as semi-replicate sampling units of each plot (Williams *et al.* 2002). Given the randomised-sampling design and because fixed objects were censused, the sampling time was irrelevant. Thus, sub-sections could be modelled as semi-replicate surveys of a plot, which provided intra-plot variability measures and satisfied most independence issues (Williams *et al.* 2002).

This assumption was tested by comparing detection and occupancy probabilities for the same data at 10, 100, 200 and 500 m resolutions. Results showed that as scale increased from 10 to 500 m, the probability of detection (p) increased, supporting the assumption that, as the size of the survey area increases, there is a naturally higher probability of detection.

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Although the detection probabilities increased when the survey resolution increased, the probability of occupancy remained the same across these scales. This indicated that, regardless of scale, the survey replicates at 10, 100, 200, or 500 m were independent, but ecologically, scale is a key factor for analyses. For example, at 10 m resolution, if bear signs are observed in any particular 10 m section, the probability is high of observing bear signs in the adjacent 10 m section because of its non-random proximate location to the first section, regardless of any random bear behaviour. Thus, independence of observations at the 10 m level is probably compromised. Further, site-occupancy could be falsely concluded, i.e. we may observe bear signs in two adjacent 10 m sections, but there may not be any other signs for several kilometres, e.g. the bear could have been simply passing through the area to or from its truly occupied site. Thus, the detection of signs at 10 m resolution may be a spurious indication of overall site-occupancy, thereby increasing the chance for Type I error.

In contrast, as the survey area increases to 500 or 1,000 m scales, there is a stronger probability that the area will be occupied and the more likely that individuals will be detected. A large scale will also include multiple habitat types, but which types are occupied or avoided cannot be determined with precision. Such low precision affects occupancy estimates in heterogeneous landscapes and conclusions of site-occupancy hold less meaning.

In this study, estimate precision was best achieved at the micro-habitat scale by multiple replicates at the 100 m sub-section level, where habitat character was more uniform and variance in both the probability of detection, p, and site-occupancy, ψ , were lowest (*see* sections 5.11 and 6.9). This scale increased the probability of detection and model accuracy of whether a bear consistently occupied a specific site. For macro-habitat scales, transect-level replicates for sites and habitat types increased estimate precision at the landscape level.

Resolution was not relevant for camera surveys, but 5-7 day trapping periods were replicate sampling occasions for each trap site. Thus, it was possible to model separately distinct photo or sign events with replicates at various scales for each site in PRESENCE. Data matrices of detection-non-detection (1, 0) histories and actual count histories were made in Excel pivot tables and imported to PRESENCE. Following detection probability procedures, transects or camera-trap sites were survey "plots" within their study areas, while 100 m sections of transects and 5-7 day camera-trapping periods were replicate surveys ("sampling occasions") for each transect or trap site. For detection-non-detection, ≥ 1 independent event/100 m section or trap site was recorded as "1" and no event was "0". All single season models were run in PRESENCE for single and multiple groups with constant *p* and survey-specific *p*, as well as the abundance-induced heterogeneity model. Akaike's Information Criteria (AIC) was used for objective selection of the most suitable model.
6.4 Sign Distribution

Clustered or aggregated habitat use is important for determining density and abundance estimates. It can also help determine micro-site influences on sun bear habitat use and patch compression effects on bear activity (i.e. concentrated or dispersed activity). This information can aid predictions of whether the frequencies and densities of signs are indications of the relative abundance of animals generating the signs.

Sign presence (1) or absence (0) were recorded in a spreadsheet column and the exact positions to 1 m resolution of all signs along their respective transects were recorded in an associated column. Data were arranged such that every row in the spreadsheet represented that particular sign's associated 10 m sub-section along the transect. Each 10 m row was cross-referenced with its allied 100, 200, and 500 m sections, transect ID, habitat type, biogeographic parameters, and so forth in adjacent columns. With this data-matrix structure, the random distribution of sun bear signs could be examined based on (1) each sign's exact position along the transect and (2) each sign's position relative to other signs, thereby determining dispersed or aggregated activity at 10 - 1,000 m scales of resolution. Two-way Chi-square analyses were run to test expected *versus* predicted values of the statistical distribution of sign presence, where a significant departure from random distribution, defined here as "clustering", was indicated by a significant P-value result.

6.4a Assumptions

The most important assumption here is that surveys were random and independent. As noted in the sign census methods (section 5.2), randomisation theory was followed, such that transect locations were based on a stratified-random design. Focal areas and sites were stratified *a priori* according to habitat type and so forth, and transects were fully randomised *a priori* in randomly numbered $1 - 2 \text{ km}^2$ grids and selected according to random numbers tables. Map coordinates for randomised transects were used to position transects in the field and starting points were positioned in entirely random locations. Transects were conducted using ramdon compass bearings according to random numbers tables. Ursidae foraging behaviours (Jonkel and Cowan 1970, Rogers 1976, 1987, Craighead *et al.* 1995, Powell *et al.* 1997) suggest bear movement patterns are at least semi-random. Hence, the likelihood of bear signs occurring at any point along a random transect was expected to be random.

Sign data were organised in spread sheet rows representing every 10 m on each transect, but possible independence issues arise at the 10 m scale of resolution, i.e. if a bear occurs in one 10 m section it is probable that signs might be observed in the adjacent 10 m section because of its non-random proximate location, irregardless of random bear

behaviour. Results showed that 100 and 200 m sections were independent and achieved good model fit (sections 5.11 and 6.9). Also, because the Chi-square test is sensitive to low expected observations, sample size (n) should be > 5. To minimise possible violations and sample size sensitivity of the Chi-square test, sign presence-absence data were grouped and tested by their allied 100 or 200 m sections (n=5 or 10 per 1,000 m transect) and by transect. Accordingly, bear sign presence was tested for random distribution. Tests were conducted at all scales relative to specific habitat types, sites, elevations, disturbances, and so forth from micro-site (10 - 500 m) levels of resolution to patch (10 - 100 ha) and landscape scales.

6.5 Density and Abundance

6.5a Bear Sign Density

Sign densities for Fixed-width censuses were based on sign frequencies in all 1,000 x 10 m transects, which provided a sample area size of 1 ha/transect. Densities were calculated by the formula: n

$$D = \frac{n}{LW}$$

where *n* is the number of observed sign events, *L* is transect length, and *W* is transect width.

Sign density estimates from Distance-sampling methods were calculated in programme DISTANCE version 4.1 release 2 (Thomas *et al.* 2003) based on the models and theory developed by Buckland *et al.* (1993, 2001). As noted in section 5.2c the Distance sampling method employed here surveyed a sample of the sign populations by using count and distance data to estimate the encounter rates and detection probabilities of signs. Probability of detection was modelled as a function of observed distances from the transect centre line using robust semi-parametric methods (Buckland *et al.* 1993, 2001). Detection functions and encounter rates were estimated separately. Models then corrected for potential bias and variability, estimated potential missed objects, and derived abundance and density estimates. Variance was estimated empirically and by non-parametric bootstrapping (Thomas *et al.* 2003). The log-likelihood function, Akaike's Information Criteria (AIC), was used for objective selection of the best fitting model with the least amount of variance.

The foundation of Distance-sampling analysis is modelling the detection function, g(y). Following Buckland *et al.* (1993, 2001), the modelling engine in programme DISTANCE implements robust key function models with an adjustment term. The available models are Uniform, Half-normal, Hazard-rate and Negative Exponential and the adjustment terms are Cosine, Simple Polynomial, and Hermite Polynomial (Thomas *et al.* 2003). The detection function is based on the following general formula (Buckland *et al.* 1993):

$$g(y) \propto key(y) \left[1 + series(y)\right] \mu = \int_{0}^{w} g(y) dy$$

where g(y) is the detection function, key(y) is the key function model, series(y) are the adjustment terms, and y is distance. The function is scaled so that g(0) = 1. The Half-normal and Hazard-rate models provided the best-fit for the current data. In the example of the detection function above, the key function is the Hazard-rate model and the adjustment is one polynomial term of order 4 (Thomas *et al.* 2003). The formula for the Hazard-rate model (HR) is described by Buckland *et al.* (2001) as:

$$HR = 1 - \exp\left(-\left(\frac{y}{\sigma}\right)^{-b}\right)$$

where σ is the scale parameter, y is distance to the object, and b is the shape parameter that fits the data to the model. The formula for the Half-normal model (HN) as described by Buckland *et al.* (2001) is:

$$HN = \exp\left(\frac{-y^2}{2\sigma^2}\right)$$

where again, σ is the scale parameter and y is distance to the object. Details on the theory and mathematical basis of these models are described by Buckland *et al.* (1993, 2001).

6.5b **Population Density**

Bear densities for various sites were estimated only from camera-trapping results as presence-absence (1, 0) or count data (number of distinct photo events). Model precision was best assured by identifying photo captures as distinct photo events that represented individual detection data (i.e. specific sightings) at each trap site. Instantaneous consecutive triggering of a camera at one site producing multiple photos of the same bear was considered one distinct photo event. The data were first modelled in programme PRESENCE (Hines 2005) to generate detection probabilities (*see* section 5.3), which produced site-occupancy probabilities (*see* section 6.3) that estimated the proportion of area occupied by bears. Estimated variance was provided by programme PRESENCE.

The site-occupancy parameter of the MacKenzie *et al.* (2002) model is a designunbiased estimate of the proportion of area occupied (ψ). Thus, the intuitive association between estimated occupied area (ψ) and independent estimates of home range (*H*) by Wong (2002) were used to generate empirically-based minimum estimates of density, *D*(min):

$$D(\min) = \frac{\Psi \times A}{H}$$

such that A is the study area. This approach generates a conservative estimator of minimum density. For home range (H), I used all published sun bear home ranges derived from radio

km² (± 6.1 SD). Each home range estimate was used to calculate different densities for each camera-trap survey site. The variance estimate for ψ was transformed to standard deviation, which was used to generate ± Standard Error (SE) for all density and population estimates.

6.5c Population Abundance

Using density estimates calculated from detection and site-occupancy probabilities as described above, area-specific abundance estimates were derived by multiplying bear density/km² by the total effective habitat (km²) available to bears in each survey site and its respective focal area (Gunung Leuser National Park, the Leuser Ecosystem, Kayan Mentarang National Park, and the Bulungan Research Forest).

Bears are not strictly territorial and will have some degree of overlap among individuals, which can affect density and abundance estimates. Accordingly, several assumptions were considered: (a) female Ursidae offspring will occasionally overlap with their mothers, (b) male Ursidae are typically more territorial than females, (c) male Ursidae will usually include at least 1 - 2 females within their home range, and (d) a 50:50 sex ratio. Abundance estimates were then calculated using three demographic scenarios based on the literature to account for variation in possible bear overlap:

- (1) N_l , Adult bears only. This minimum estimate is based on a mean home range of 14.8 km² (± 6.1 SD) (Wong 2002) and 1 bear/range with no range overlap.
- (2) N_2 , 50% overlap. Wong's (2002) telemetry study in Sabah showed four male sun bears had a mean home range of 14.8 km² (± 6.1 SD) with overlap of 3.2 – 22.17%. While 15 – 20% overlap is realistic (Craighead *et al.* 1995, Powell *et al.* 1997, Servheen *et al.* 1999), a population estimate using a liberal overlap of 50% was calculated to account for missed individuals and under-estimation.
- (3) N_3 , 1 male + 1 female + 1 cub/female. It is known through zoo studies that one female sun bear can produce an average of 1 2 cubs every 2 3 years. General studies of wild Ursidae show ca. 50% cub survival to reproductive age among the sun bear's closest phylogenetic relatives. Thus, an estimate was calculated based on 2 adults (1 male per female) accompanied by one cub, thereby tripling the original N₁ estimate.

It is important to note that Wong observed a 66% loss of telemetry-captured individuals, half of which were known mortalities. Thus, cub recruitment may be replacing adult mortalities.

Population analyses were also used to help predict sun bear habitat and landscape uses by examining questions like: What is the relative degree of sun bear habitat use, e.g. what are density and abundance levels for specific habitats, biogeographic conditions, etc? If sun bear habitat is fragmented and lost over time, what movement barriers exist and where are potential suitable corridors and core habitat patches in specific landscape configurations to sustain individual fitness, metapopulation viability, and evolutionary potential over time?

6.5d Assumptions

Perhaps the most important assumptions of this approach rest in (A) detection probabilities, (B) associated site-occupancy probabilities, (C) accuracy and limited number of home range estimates from another study and their generalisation to other bears, and (D) the reality of animal distributions. Assumptions of detection and site-occupancy probabilities are addressed by the MacKenzie *et al.* (2002) model and are discussed in relevant sections.

Home ranges clearly vary within populations and species, and the home range estimates used here were from a limited sample of bears (n=4) from another study and area on Borneo by Wong (2002) using conventional radio-telemetry methods that have inherent assumptions and error. Range and distribution variances can depend on the bear's life history, individual behaviour, population density, environmental characteristics of its range, and so forth. None of these influences can be controlled and one way to minimise error in generalised applications of this type of data is by using means. In this study, the only published mean home range for sun bears, along with each range estimate and three demographic scenarios to account for variation in bear overlap, were used to calculate alternative densities and abundances. Thus, these multiple estimates provide the reader with a range of possible densities and abundances that are empirically-based. Given high landscape variance and disparate distributions in other parts of the sun bear's range in South-East Asia, these estimates are only for the focal areas studied here and are not generalised.

Patchy distributions also affect density estimates and few species or taxa, if any, occupy 100% of their range and have perfectly uniform distributions. Most individuals in a population have different ranges varying across seasons, years, and habitats – often with gaps between individual ranges. Patchy distributions can affect density estimates that do not account for fragmented distributions of individuals at the habitat and micro-site levels within patches. Such limitations were addressed by (1) accounting for patchiness and gaps by using only the estimated proportion of area occupied based on empirical data and robust theory and models, (2) generating density estimates from actual home range sizes as well as the mean, and (3) limiting estimates only to these study areas. But, these estimates do not account for the precise degree of patchiness among bears and models and home range estimates rely on assumptions. Thus, results assume a degree of inference. These empirically-based data and analyses are supported by robust sampling designs and theory, but it is stressed that resulting population figures must be viewed cautiously as estimates with related assumption and error.

6.6 Contrasting Probability Differences

Sauer and Williams (1989) developed a general matrix multiplication and inversion procedure for the comparison of rate estimates that incorporates associated variance and covariance estimates. As described by Hines and Sauer (2004) a *z*-test can be used to compare two such rates. The *z*-test compares a series of constants in a contrast, with the limitation that the sum of the contrast = 0 and is applicable to a variety of hypotheses, such that simple contrasts can be used to specify groupings of rates, but it is limited when examining differences among more than 2 groups (Hines and Sauer 2004). Where n > 2 groups, such as in a composite hypothesis and in this study, Sauer and Williams (1989) suggested an asymptotic chi-square quadratic form. For a composite hypothesis, the null hypothesis is rejected with the probability that the observed chi-square is greater than a tabular critical value of chi-square, with degrees of freedom determined by the choice of the contrast matrix and significance level (Sauer and Williams 1989).

This procedure was used in this study to compare detection probabilities and siteoccupancy rates in the software programme CONTRAST version 2 (Hines 2004). Probability rates and associated variances were first generated in programme PRESENCE (Hines 2004) based on models developed by MacKenzie *et al.* (2002). Variances provided in PRESENCE were then transformed to standard errors in Excel spreadsheets and entered along with their associated probabilities into programme CONTRAST.

Probability rates of two or more groups were then compared statistically in programme CONTRAST based on the asymptotic quadratic Chi-square function. CONTRAST was used to achieve this by assigning each of the rates to its associated group (e.g. detection probabilities of bear sign in primary forest, secondary forest, and so forth) and then testing the null hypothesis that there is no difference among groups (Hines 2004). The program engine conducts an asymptotic quadratic chi-square test of differences among the rates from different groups and provides a P-value for significant differences along with degrees of freedom.

<u>Limitations</u>: The primary limitation of this procedure is that it was used to test probabilities, which are estimated proportions with inherent variance from their own generation. Contrast minimises this limitation by testing the proportions along with their standard errors in both overall general tests among all probabilities and in specific tests between probabilities.

RESULTS

6.7 <u>Camera Trapping</u>

A total of 10 camera-trapping surveys were conducted at different sites in northern Sumatra and East Kalimantan. Six sites were located in the Leuser Ecosystem where surveys were conducted from 11 November 2001 to 5 May 2004 in a diverse representation of habitats and disturbances at trap sites ranging from 47 to 2,657 m asl. The first survey in Leuser, which was conducted at Ketambe, was limited to half the number of sites and was halted early due to rebel activity in Aceh province. All other surveys were complete. On Borneo, two surveys at two sites inside and bordering Kayan Mentarang National Park were conducted from 7 March to 6 July 2003 in trap sites ranging from 340 to 1,259 m asl. The final two surveys were conducted in the eastern region of the Bulungan ecosystem at two sites from 14 July to 9 November 2003 in trap sites ranging from 105 to 797 m asl.

All surveys in Leuser operated continuously for 8 - 10 weeks 24 hours/day. In East Kalimantan, logistics demanded that surveys be conducted continuously for 7 - 8 week periods 24 hours/day. Trapping effort is provided in table 6.1. A total of 280 camera trap stations operated over 15,897 trap nights and produced 10,804 photos, of which 4,564 photos had animal subjects. Bear captures (n=171 photos) comprised 3.6% of all animal photos, 62% of which (n=107 photos) were distinct photo events. Examples of photo captures are in Appendix 1. About 57% of all photos did not appear to be triggered by animals due to:

- (1) environmental conditions (e.g., light, moving twigs, falling leaves) triggering active infra-red sensors,
- (2) electronic malfunction of equipment because of age, wear, humidity/water, animal damage, and so forth,
- (3) insects triggering active infrared sensors (e.g. moths and butterflies passing through the beam; ants and termites walking on the beam window on units), or
- (4) human error (e.g. active infra-red beam not being centred).

Furthermore, evidence in some photos indicated some cameras were triggered by an animal moving too quickly for the small, but noticeable, trigger-to-camera delay to capture.

Table 6.1 Camera-trapping effort in all study sites during 11 November 2001 - 5 May 2005.

Focal Area	Site	Elevation (m asl)	Survey Period	Camera Stations	Trap Nights	Total Photos	Animal Photos	Bear Photos	Distinct Bear Photo Events
	Ketambe	433 - 2,002	11 Nov – 8 Dec 01	17	476	240	119	0	0
	Sei Badak	50 - 210	15 Mar - 30 May 02	33	1,848	1,264	717	22	17
Leuser	Sei Birah	211 - 964	9 Sept – 8 Dec 01	32	2,240	1,630	540	36	28
Ecosystem	Ketambe Atas	1,217 - 2,657	2 Mar – 26 May 03	35	2,205	1,011	321	18	8
	Sekundur	47 - 107	15 Aug – 18 Oct 03	35	1,960	1,566	402	0	0
	Gunung Putar	1,402 - 2,113	5 Feb – 5 May 04	32	1,792	820	366	6	3
Kayan Mentarang /	Lalut Birai	340 - 1,013	7 Mar – 1 May 03	24	1,344	1,177	500	11	7
West Bulungan	Ulu Nnggeng	450 - 1,259	14 May – 6 July 03	24	1,344	1,159	556	49	22
East	Seturan	105 - 257	15 July – 8 Sept 03	24	1,344	1,202	736	12	8
Bulungan	Tukuk Mawot	220 - 797	16 Sept – 9 Nov 03	24	1,344	735	307	17	14
			280	15,897	10,804	4,564	171	107	

6.7a. Northern Sumatra

In the Sumatran survey sites, a total of 6,531 photos were taken over 10,521 trap nights. Photographs of wildlife totalled 2,465 and local hunter/gatherers unknowingly triggered 28 photos. Six camera units were stolen during this study, of which four were returned. Table 6.2 lists species captured in Leuser. Of a total of 59 genera, 56 were identified to the species level. There were 82 bear photos at four of the six sites, of which 56 photos were independent photo events. All of these photos were in undisturbed primary forests falling within the mean biophysical traits discussed in chapter 5, where older more heterogeneous primary forest traits, such as high canopy cover (>95%) and refugia (> level 3), low ground cover (<20%), high tree species diversity, and mature stand structure predominated. Two surveys in Leuser (Ketambe and Sekunder) did not produce any photo captures of bears or tigers over a combined total of 2,436 trap nights. These surveys were conducted in secondary forests ranging in age from 1 - 25 years old and in primary forests subjected to and affected by a range of habitat disturbances, including logging, illegal gardens, and human activities within and adjacent to these primary forest sites.

There were a total of n=9 independent tiger captures, from which 6 tigers were positively identified by their unique striping patterns in 11 distinct photo events totalling 25 photos at the same four survey areas where sun bears were captured.. Two other tigers were unidentified, which could have been different tigers or any of the other six. Thus, the minimum number of individuals in the 384 km² study area was 6 tigers. The majority of tiger captures were in the more remote and high elevation site of Ketambe Atas in Aceh. There were 55 photo captures of clouded leopards, where 76% were in the remote undisturbed site of Sei Birah. The majority (87%) of marbled cat and banded linsang photos (58%) were also in Sei Birah. Leopard cat captures were rare and Asiatic golden cat were present at all study sites.

Table 6.2. Species captured by remote cameras at the six study sites in Sumatra (continued on next page).

Species	Gunung Putar	Ketambe	Ketambe Atas	Sei Badak	Sei Birah	Sekundur	TOTALS
Arborophila rubrirostris	1						1
Arctictis binturong		1		2	3	3	9
Acrtogalidia trivirgata	4			1			5
Arctonyx collaris	13	2	15				30
Argusianus argus		20		138	93	152	403
Brachypteryx montana			1				1
Capricornis sumatraensis	113						113
Cervus unicolor				17	2		19
Chalcophaps indica						1	1
Copsychus malabaricus				10			10
Corvus enca		1					1
Cuon alpinus					1		1
Diplogale derbyanus			1	9	14	9	33
Echinosorex gymnurus				7	5	2	14
Elephas maximus					4	11	15
Erithacus cyane				26	14		40
Felis bengalensis				4		2	6
Felis temminckii	15	10	14	11	10	6	66
Helarctos malayanus	6		18	22	36		82
Herpestes spp.				4		1	5
Hystrix brachyuran		15	22	141	188	65	431
Lariscus insignis					6		6
Leopoldamys sabanus			5	2	7	1	15
Lophura inornata	10	10	8				28
Macaca fasicularis		2		7	4	9	22
Macaca nemestrina	9	8	4	119	21	61	222
Manis javanicus				1	2	1	4
Martes flavigula	9	1	13		1		24
Maxomys hylomyoides	3						3
Muntiacus muntjac	117	20	153	9	6	8	313
Myophoneus glaucinus castaneus	6						6
Naemorhedus sumatrensis		7	28	2	3		40
Napothera marmorata			1				1

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Gunung Putar Ketambe Ketambe Atas Sei Badak Sei Birah Sekundur TOTALS Species Neofelis nebulosa Paguma larvata Panthera tigris sumatrae Paradoxurus hermaphroditis Pardofelis marmorata Pitta granatina Pitta sordida Polyplectron chalcurum Pongo abelii Presbytis thomasi Prionodon linsang Python reticulatus Ratufa affinis Rhizothera longirostris Rollulus rouloul Rollulus spp. Sundamys infratluteus Sundasciurus spp. Sus scrofa Tragulus javanicus Tragulus napu Treron vernans Tupaia tana Unknown Varanus salvator Zoothera sibirica TOTALS

Table 6.2 (continued). Species captured by remote cameras at the six study sites in Sumatra.

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Bootstrap randomisation tests (Sohaw 1993) of species diversity using four main diversity indices (Shannon-Wiener *H*, Simpson's D, Margelef *D*, and Fisher's Alpha) (PISCES 2002) as well as the Rényi diversity ordering index (figure 6.1) in PISCES showed that overall the most diverse sites in Leuser were Sei Birah and Sei Badak, with 33 and 32 species captured, respectively. Not surprisingly, the higher elevation sites, Gunung Putar (1,402 - 2,351 m asl) and Ketambe Atas (1,217 - 2,657 m asl), were less diverse. Although the mid-elevation area of Ketambe has been known historically as a highly-diverse ecological community supporting tigers, sun bears, rhinoceros, orang-utans, and many other large mammals, it did not produce any bear or tiger photo captures. This area has suffered a notable influx of human activity, hunting, and logging over the past 15 - 20 years (Robertson and van Schaik 2001) and photo captures at this site were the lowest in species diversity in our Leuser study areas. The more remote and higher altitudes in the same ecosystem produced more diverse animal captures, despite normally decreasing diversity at higher elevations. The 23 year-old secondary forests of Sekundur did not produce any bear or tiger photos, but was moderately diverse in other species.



Figure 6.1. The Rényi diversity (Rényi, 1961) ordering index for animal species captured by remote camera trapping in the Leuser Ecosystem.

6.7b East Kalimantan

In the East Kalimantan survey sites, a total of 4,273 photos were taken over 5,376 trap nights (table 6.3). Photographs of animals totalled 2,099. Local hunters triggered 50 photos and hunting dogs triggered 27 photos. Of a total of 63 genera or families, 50 were identified to the species level. There were 89 total bear photos among the four sites, of which 51 photos were distinct photo capture events. As in Sumatra, all bear photos were located in undisturbed primary forests with mature stand structure and there were no captures in young secondary forests, edge habitats, logged sites, agricultural areas, or other disturbed sites.

There were a total of nine clouded leopard photo captures, which were in undisturbed primary forest, three of which were distinct capture events. Two of the latter were in the remote area of Ulu Nnggeng in Kayan Mentarang National Park while the third was in primary forest ca. 1 km from RIL logged sites in East Bulungan. Four photos of banded linsang were recorded in the undisturbed lowland forests of the Bulungan Research Forest. Three of these photos were distinct capture events. Only one photo capture of a bay cat and marbled cat each occurred in the East Kalimantan study sites. Both were in the Ulu Stee area of Kayan Mentarang National Park. The bay cat photo was the first known photo capture of this species in the wild. There were multiple captures of leopard cats, but again these occurred only in undisturbed primary forests.

Bootstrap randomisation tests (Solow 1993) in PISCES of species diversity using the Shannon-Wiener *H* and Simpson's *D* indices indicated the interior Ulu Nnggeng region of Kayan Mentarang was the most diverse area (H = 2.836 and D = 10.98), whereas the Margelef *D* (D = 7.01) and Fisher's Alpha ($\alpha = 11.34$) indices showed the primary undisturbed sites of Seturan were just slightly more diverse. In both cases, the most remote and protected sites reflected the most diverse photo captures. Table 6.3 lists the species captured at respective sites in East Kalimantan. Slightly more species (n=47 species) were captured in the most diverse sites (Seturan) of the Bulungan Research Forest than in the most diverse sites (Ulu Nnggeng) in Kayan Mentarang (n=43 species).

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Species	Ulu Nnggeng	Lalut Birai	Seturan	Seturan	TOTALS
1	2	4	(Tukuk Mowat)	(KIL/CIVV Forest)	17
Arcticus binturong	3	4		10	1/
Arctogaliaa trivirgata	20	10	52	1	1
Argusianus argus	20	18	53	60	151
Caloperdix oculea	2				2
Cervus unicolor		3		l	4
Copsychus malabaricus				6	6
Cuculus vagans				2	2
Cynogale bennettii				1	1
Diplogale derbyanus	3				3
Echinosorex gymnurus	2	1		4	7
Felis badia	1				1
Felis bengalensis	14	2	5	5	26
Felis marmorata	1				1
Haematortyx saguiniceps	1				1
Helarctos malayanus	49	11	17	12	89
Hemigalus derbyanus	16	2	11	10	39
Herpestes brachyurus	25	4	19	7	55
Herpestes hosei	3		2		5
Herpestes spp.	7	5	29	2	43
<i>Hystricidae</i> spp.		2			2
Hystrix brachyuran	94	17	16	2	129
Lophura bulweri			5	1	6
Lophura ignite nobilis	5	7	6	175	193
Lophura inornata	1		2	2	5
Lophura spp.	1				1
Macaca fascicularis	4	15		25	44
Macaca nemestrina	49	146	50	104	349
Macaca spp.		1			1
Manis javanica				5	5
Martes flavigula	11	3	4	3	21
Muntiacus atherodes	14	84	13	13	124
Muntiacus muntjac	18	24	16	29	87
Muntiacus spp.	2	2	2	1	7
Muridae spp.		1		8	9

Table 6.3. Species captured by remote cameras at the four study sites in East Kalimantan. The most remote sites reflect the most diverse photo captures (continued on next page).

Table 6.3 (continued). Species captured by remote cameras at the four study sites in East Kalimantan. The most remote sites reflect the most diverse photo captures.

Species	Ulu Nnggeng	Lalut Birai	Seturan (Tukuk Mowat)	Seturan (RIL/CNV Forest)	TOTALS
Neofelis nebulosa	2			7	9
Ophiophagus Hannah		1			1
Paguma larvata	5	1	2		8
Pandion haliaetus	2				2
Paradoxurus hermaphroditus	1	2		1	4
Pardofelis marmorata			10		10
Petinomys setosus				1	1
Pitta granatina				12	12
Pitta guajana	9	1		2	12
Pitta spp.	1			1	2
Presbytis hosei hosei	4		2	2	8
Presbytis spp.				1	1
Prionodon linsang			1	3	4
Rheithrosciurus macrotis	3	5	1	3	12
Rollulus rouloul	20	1	1	48	70
Snake spp.				1	1
Sundasciurus hippurus	1			6	7
Sundasciurus spp.	2			3	5
Sus barbatus	3	2		3	8
Tarsius bancanus borneanus				1	1
Thecurus crassispinis	1	18		52	71
Tragulus javanicus	4			18	22
Tragulus napu	37	86	1	2	126
Tragulus spp.		1		2	3
Trichys fasciulata	2		1	15	18
Unknown	14	2	4	30	50
Varanus salvator	1				1
Viverra tangalunga	97	27	34	33	191
Viverridae spp.	1	1			2
TOTALS	556	500	307	736	2099

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An important measure of diversity is heterogeneity based on the dominance of particular species. In this case, the Berger-Parker Dominance index showed that the Ulu Nnggeng region was the most heterogeneous in species captures with the least amount of dominance by any specific genus or species. A variety of avian species were present in the Seturan lowland sites, particularly ground birds, such as pheasants and partridges, that were absent in the mid- to upper-elevation areas of Kayan Mentarang. These species produced many more photo events in the BRF than in the Kayan Mentarang surveys and, thus, influenced the capture indices. The CNV- and RIL-logged areas of Seturan were the least diverse. The Rényi diversity ordering index showed that the undisturbed primary forests in the Ulu Nnggeng were the most diverse by a small margin over the lowland forests of Seturan (figure 6.2).



Figure 6.2. The Rényi diversity (Rényi 1961) ordering index for animal species captured by remote camera trapping in the East Kalimantan study sites.

6.8 Genetic Analyses

All genetic samples (table 6.4) were found in low- to mid-elevation mature primary forest at 137 - 1,010 m asl in 95 - 100% canopy cover. No samples were found in secondary forest or disturbed areas. Samples that could be amplified and resulted in identifiable individuals were collected at elevations of 385 - 777 m asl. A total of only 40 scats and 8 hair samples were found, of which 11 were collected along transects while the rest were located during pre- and post-transect surveying. All scat samples were stored in ethanol and hair in indicating silica according to standard protocols *(see* Methods section 6.1), but DNA from only 25 samples (17 scat and 8 hair samples) was usable (table 6.4). It is possible that the 4:1 ratio of ethanol to scat was too low.

Tests of domestic dog faeces at the East Kalimantan study sites showed that the average scat in this area disappeared within 24 - 48 hours, with a minimum time of 1 hour. The primary cause of loss was predation or deterioration from environmental exposure, particularly rain. Tests of sun bear hair-snagging by G. Fredriksson (pers. comm.) showed that traditional hair-snagging methods were not useful for sun bears. Sun bears have the shortest hair of all Ursidae and even concerted pulling of hair on sedated sun bears produces few hairs with root follicles that are genetically-analysable (pers. obs.). Thus, because a major component of this study was genetic sampling of bear scat and hair, concentrated efforts were devoted to scat and hair search images during all surveys. Intensive ground searches were conducted for scat along every metre of the transects. In addition, every nest and all trees with claw marks were scanned for hairs. These searches reduced our census pace to a mean of < 0.13 km/hour. The 11 genetic samples collected on transects comprised only 0.22% of all observed signs along 335 km of transects in 28 months. Other workers have collected more scats (Meijaard et al. 2005), but this occurred over longer periods (ca. 5 years) and primarily on trail systems in small insular forest reserves less than $100 - 200 \text{ km}^2$ in size, which concentrated bear activity in small areas. In vast forested sites $> 4,000 \text{ km}^2$ such as in this study, bear activity was far more dispersed, particularly off trails, and it is reasonable to conclude that the probability of observing bear scat or hair was low.

<u>Micro-Satellite Amplification</u>: Samples were tested at the University of Idaho by Dr Lisette Waits (Waits 2003) using a duplicated BL PCR duplex. Peak presence was high, but results were inconsistent between duplicated samples and successful B peaks (blue dye), which often drown out any L peaks (green dye), because the two loci are about the same length (Waits 2003). Samples that showed any sign of success with the BL duplex were re-PCRed using B, L, and AC. Success rates did not improve for B or L. The AC duplex also

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had very low success rates (1 A and 4 C) and the samples were re-run using the A and C PCRs duplicated. The A PCR failed to amplify any samples other than the positive. The C PCR had 3 amplifications in which one of the two copies amplified and 2 amplifications in which both copies amplified, but the results for the amplifications did not match. Poor DNA quality resulted in inconsistent results and individual ID using micro-satellites was stopped.

Mitochondrial Sequencing: Seven of the samples were successfully amplified, of which 4 were scat samples and 3 were hair samples (table 6.4). One hair sample amplified as a felid with a 94% match of haplotypes from a domestic cat *(Felis domesticus)* and a wild cat *(Felis silvestris)*. The remaining 6 samples were sun bears. Two of the haplotypes were an exact match and the others were unique. Individual IDs were not successful using micro-satellites, but 5 different individuals could be distinguished with mtDNA sequence data. Four of these individuals were located in the Kayan Mentarang study sites and one was from Tankahan in Leuser. Sequence data are provided in Appendix 2.

On Borneo, hair samples L2 and L3 identified the same individual (SB1) and were collected in the Jalungkereng site of Kayan Mentarang National Park 970 m apart. Bear SB2 was located in the Tankahan study area of the Leuser ecosystem adjacent to a wildlife trail. This was the only genetic sample amplified from Sumatra. Bear SB3 was found in the Lalut Birai study area 2,105 m east of bear SB1. Bear SB4 was identified 1 km south of bear SB3 and 2,000 meters east of bear SB1. Finally, bear SB5 was identified in the Ulu Stee study area about 10 km interior from the Lalut Birai research station and 7 km west of the closest identified bear (SB1). These reported distances are in GPS aerial extent.

Although the number of successfully-amplified samples was few, there are several important results of this work. Methodologically, we learned that the sampling protocols used in this study are the best available for this species and in tropical forests and, under the proper conditions, mitochondrial sequencing will provide identification of individual sun bears. Storage protocols indicate that a stronger ratio of ethanol to scat would be better. Uncontrollable environmental conditions, including sample predation and exposure, limited the quantity and quality of samples prior to collection. Both of these problems, particularly exposure, have been found with other tropical bears (Waits pers. comm.). Analytically, the methods were able to distinguish five distinct sun bears. As discussed below, these data were used to (a) gauge relative sign density, (b) correlate with camera trapping and sign census results, and (c) estimate potential range overlap. Phylogenetic analyses are being conducted from these samples relative to sun bear and Ursidae samples from other studies, but lab results were not available at the time of this writing (Waits pers. comm.).

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Table 6.4. Summary of usable sun bear genetic samples during September 2001 – May 2003. All samples were located in primary lowland rainforest with 100% canopy cover.

Sample Type	Field ID	Date Collected	Location	Elevation of Sample (m asl)	Extraction Date	Micro-Satellite Amplification Success	Mitochondrial Sequencing Success	Species	Individual ID
Hair	K1	11-09-01	Ketambe	433	12/16 - 17/03	no	no		
Hair	K2	11-09-01	Ketambe	433	12/16 - 17/03	no	yes	Felid	F1
Hair	K3	28-09-01	Ketambe	505	12/16 - 17/03	no	no		
Hair	A1	14-02-01	Sei Badak	172	12/16 - 17/03	no	no		
Hair	L1	30-04-02	Birai	485	12/16 - 17/03	no	no		
Hair	L2	18-10-02	Birai	429	12/16 - 17/03	no	yes	Sun bear	SB1
Hair	L3	18-10-02	Birai	502	12/16 - 17/03	no	yes	Sun bear	SB1
Hair	L4	14-05-03	E Bahau	405	12/16 - 17/03	no	no		
Scat	K1	08-09-01	Ketambe	600	3/13/03	no	no		
Scat	K2	19-09-01	Ketambe	515	3/13/03	no	no		
Scat	A1	20-01-02	Sei Badak	105	3/13/03	no	no		
Scat	A2	07-02-02	Sei Badak	137	3/13/03	no	no		
Scat	A3	26-03-02	Sei Badak	174	3/13/03	no	no		
Scat	T1	28-09-02	Tankahan	777	3/13/03	no	no		
Scat	T2	26-10-02	Tankahan	600	3/13/03	no	yes	Sun bear	SB2
Scat	L1	26-04-02	Birai	385	3/13/03	no	yes	Sun bear	SB3
Scat	L2	30-04-02	Birai	475	3/13/03	no	no		
Scat	L3	05-01-02	Birai	460	3/13/03	no	no		
Scat	L4	02-05-02	Birai	545	3/13/03	no	no		
Scat	L5	18-10-02	Birai	502	3/13/03	no	yes	Sun bear	SB4
Scat	L6	20-11-02	Ulu	514	12/12/03	no	no		
Scat	L7	29-01-03	Ulu	651	12/12/03	no	no		
Scat	L8	26-05-03	Ulu	590	12/12/03	no	yes	Sun bear	SB5
Scat	L9	17-05-03	Ulu	1010	12/12/03	no	no		
Scat	L10	17-05-03	Ulu	900	12/12/03	no	no		

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6.9 Sun Bear Habitat Use

6.9a Habitat Disturbance

Bear behaviour, movements, and persistence are influenced by food, physical health, environment, cover, and habitat quality. The original *a priori* objective of this work was to examine and test habitat disturbance as only one of many parameters that could potentially influence sun bear landscape use. Yet, tests revealed that habitat disturbance (i.e. logged forests, agricultural areas, roads, edges, villages, large high-traffic human trails, and so forth) was consistently the most dominant interactive influence on sun bear habitat use, including in primary forest when disturbance was within 5 km of bear activity. The significant majority of bear signs (92.7%) were observed in undisturbed forest regardless of site ($r^2=0.722$, F=1635.20, df=49, P<0.0001), such that in areas with higher intensities and extents of disturbance, fewer bear signs were observed (figure 6.3). Further, despite thousands of hours of effort with extensive geographic coverage in a wide variety of habitat types, no photographs or genetic samples were observed in secondary forests of any age, or in CNV-logged forests, agricultural areas, roads, edge habitats, or other disturbed areas.



Figure 6.3. Comparison of total observed signs in primary forest versus disturbed areas.

Results demonstrate that the direct and interactive effects of habitat disturbance were consistently the most significant influences across all other variables and tests, regardless of habitat type, biogeographic condition, site, focal area, or region. Habitat disturbance clearly affected the distribution and abundance of sun bear signs, photographs, and genetic samples. Regression analyses revealed that distance from the edge of disturbance was the strongest influence (figure 6.4), but distance effects were dependent on disturbance intensity (i.e. when > 25% of the area was disturbed), type, age, and geographic extent. These latter interactions accounted for at least 85% of the variation in sun bear signs (figure 6.5) when examined by GLM procedures separately from other biogeographic variables (r^2 =0.851, F=1413.37, df=121, P<0.0001).



Disturbance Distance Classes (m)

Figure 6.4. Logistic regression of bear activity relative to distance classes from any form of habitat disturbance of any age.



Figure 6.5. Plot of observed *versus* predicted values of total sign abundance as affected by the type, geographic extent, age, and distance of disturbance. There was a very strong relationship between habitat disturbance and bear activity, particularly if disturbance was young. The most important interactive effect was the distance and age of the disturbance relative to where and when bears were active. Note: Regression line added for graphic visual aid.

Disturbance age was also a notable effect in the model (F=216.5, P<0.0001), such that bear activity was significantly higher in more regenerated stands, beginning with minor transient or exploratory activities after 15 years (figure 6.6). In stands that had regenerated at least 20 - 25 years, bear activity levels were low to moderate, but insignificant relative to primary forest. The significant majority of bear activity in post-disturbed sites, as observed by sign and camera surveys, was in older forests of more advanced seral stages that retained similar structural characteristics to primary forests. Depending on the intensity and extent of the disturbance, sites allowed to regenerate and produce cover and a diversity of food resources had significantly more bear activity.



Figure 6.6. Total bear signs/ha relative to forest age in months after disturbance. Disturbed forest ages ranged between 0 - 300 months (0 - 25 years). Sites with more advanced forest succession had more bear signs, beginning with minor activity after 180 months. Only minor transient activity (i.e. passing through area) was observed in a few areas < 180 months old. After 240 - 300 months, bear activity was moderate, but insignificant relative to primary forest. Undisturbed primary forest is generally assumed to be in old-growth seral stages in these areas (Whitten *et al.* 2000, MacKinnon *et al.* 1996). Total bear signs/ha in primary forest are in the same age class, arbitrarily "400" in this plot.

The most dominant effects in these models was the interaction between the distance (F=6116.52, P<0.0001) and timing (F=216.5, P<0.0001) of the disturbance relative to where and when bears were active. Bears avoided highly disturbed areas < 15 years old, but as figure 6.7 illustrates, as the distance from habitat disturbance increased, the relative importance of disturbance age declined in the GLM and the level of bear activity increased significantly (r^2 =0.742, F=1736.56, df=50, P<0.0001).



Figure 6.7. Bear activity relative to distance from habitat disturbance (> 25% area disturbed) of any age. Bears avoided highly disturbed areas < 15 years old. As the distance from habitat disturbance increased, the relative importance of disturbance age declined and the level of bear activity increased significantly.

When habitat disturbance was tested in models with all biogeographic parameters and human presence, habitat disturbance was consistently the most dominant interactive effect accounting for the significant majority of the variance in bear signs ($r^2=0.802$, F=1313.17, df=95, P<0.0001). The distance and timing of the disturbance relative to where and when bears were active remained the most significant interaction in these models.

A key aspect of these surveys and subsequent analyses was aging signs in the field, particularly relative to disturbance or other variables, such as the presence of people, predators or competitors. In other studies, workers have observed signs in young secondary forests, disturbed areas, edge forests, and so forth and inferred that bears were present in high numbers. In the few disturbed areas where signs were observed in the current study, 93.6% were made by bears *before* the disturbance occurred (*see* section 5.12). Of all 4,886 signs observed, only 2.4% (n=118) were generated within 50 m of disturbed areas < 1 year old (figure 6.8)).

When examined on a disturbance-elevation gradient, all disturbances were < 508 m asl, whereas the significant majority of bear signs were between 500 - 1,000 m asl (figure 6.9). This remained a significant relationship in a mixed model when controlling for the fixed-effects of habitat type at general (F=4003.55, df=8, P<0.0001) or alpha-scales (F=1625.2, df=49, P<0.0001).



Figure 6.8. Comparison of total sign occurrence in undisturbed *vs.* disturbed sites within 1 year of disturbance.



Figure 6.9. Mean bear signs/ha relative to elevation and disturbance location. Surveys ranged between 28 - 1,829 m asl. Bear activity increased with elevation and the significant majority of signs were located between 500 - 1,000 m asl, whereas all disturbances were located < 508 m asl.

Assuming that the stratified-random study design, large number of random independent surveys in multiple habitats and sites, and method plurality accounted for an appropriate degree of individual variation and habitat bias, it can be inferred that sign abundance and distribution were an appropriate relative measures of bear habitat use. Given the highly consistent and corroborative results across all parameters and tests in all habitat types, it is clear that habitat disturbance was the most significant and dominant effect on sun bear habitat use, movement patterns, and distribution in these sites.

6.9b Bear Sign Distribution

Chi-square analyses were run to test whether sun bear signs were randomly distributed or clustered within and between specific habitat types, elevations, and disturbances. In this test, a significant departure from random distribution, defined as "clustering", was indicated by a significant P-value result.

Transect locations in this study were based on a stratified-random design, such that focal areas and sites were determined a priori and then randomly-numbered transects were randomly positioned in randomly numbered 1 or 2 km² grids and in the field using random compass directions. Observations of Ursidae foraging behaviour (Jonkel and Cowan 1970, Rogers 1976, 1977, Jonkel 1984, Augeri 1994, Craighead et al. 1995, Mace and Waller 1997, Powell et al. 1997) suggest that bear movement patterns are at least semi-random. Hence, the likelihood of observing bear sign at any point along a transect was expected to be random. Possible independence issues arose at the 10 m scale of resolution, i.e. if a bear sign occurred in one 10 m section, it is probable that sign(s) might be observed in the adjacent 10 m section because of its non-random proximate location, regardless of any random bear behaviour. Chi-square tests of sign distribution supported this assumption, where as many as 55.9% of transects had statistically-significant clustering of bear signs at the 10 m scale of resolution. Thus, independence of observations at 10 m was probably compromised. If bear sign(s) was observed in a 100 m or 200 m section, the random chance of detecting bear sign(s) 100 m away was lower than at 10 m due to the bears' random movements and omnivorous or fauni-fruigivous feeding strategy. Chi-square tests showed that sign aggregation declined significantly (F=1.7, df =19, P=0.029) to 34.4% at the 200 m resolution and 40.8% at the 100 m resolution. There was a statistically-significant lower chance of observing bear sign(s) in an adjacent 100 m or 200 m section, thereby increasing the likelihood of section independence. Thus, analyses were more salient using 100 m and 200 m scales of resolutions.

Table 6.5. Chi-square tests of sun bear sign distribution at 100 - 200 m levels of resolution and the most conservative results are reported. RIL = Reduced Impact Logging and CNV = Conventional Logging practices. Clustering is indicated by significant P-values, whereas randomly distributed signs result in insignificant X^2 values.

Habitat or Disturbance Type	X ²	df	P-value
Primary Forest	12.167	9	0.2041
Undisturbed Sites	2.69	4	0.6109
Disturbed Sites	14.108	4	0.007
Secondary Forest (5-25 yrs old)	21.717	9	0.0098
Edge Forest	22.101	9	0.0086
RIL Primary Forest	18.356	4	0.0293
CNV Primary Forest	22.001	9	0.0089

According to these analyses, sun bear signs were distributed randomly in primary lowland and mid-elevation forest (table 6.5), regardless of whether this was tested at 100 m or 200 m scales of resolution. In contrast, bear signs in 5 – 25 year-old secondary forest, edge forests, swamps, and primary montane forests were clustered. Signs were randomly distributed in undisturbed sites, but sign aggregation increased in areas with higher levels of disturbance, including in primary forests subject to either conventional logging (CNV) or reduced impact logging (RIL). These differences were significant among disturbances (X^2 =2915.68, df=49, P<0.0001) and disturbed habitat types (X^2 =1583.28, df=8, P<0.0001).

6.9c Habitat Compression

As noted above, distribution tests demonstrated that sun bear signs in contiguous undisturbed primary forests were randomly dispersed within patches and sites, but they were significantly aggregated or "clustered" within the majority of disturbed, secondary, and edge habitat types (table 6.5). In these analyses, sign frequencies refer to the abundance of signs while densities refer to the amount of signs/unit area. In those post-disturbed areas where signs did occur, sign frequencies/transect were significantly lower while sign densities/ha were higher. Test results of Distance sampling data across all transects in programme DISTANCE revealed that encounter rates in post-disturbed sites were significantly higher by more than 58%, suggesting more aggregated sign.

Results suggest possible density-dependent spatial patterning among individuals. When analysed only by unit area on transects where bear signs were observed, there were 3,961 sun bear signs dispersed across 135.5 km of surveyed primary forest, for a mean density of 29.23 signs/ha. Despite a similar number of surveys in secondary forests and small primary forest patches adjacent to disturbance, signs occurred along only 15.7 km with a much higher mean density of 58.92 signs/ha. Areas affected by disturbance, particularly small forest patches, had more densely clustered, homogeneous bear size classes, and the signs were of similar age and apparent origin.

High density in the latter areas was not from clustered forage. More than 86% of transects had significantly dispersed forage cover ($\bar{x} = 1.98 \pm 0.0035$ SE) from 100 m ($r^2=0.523$, F=110.66, df=303, P<0.0001) to 1,000 m scales ($r^2=0.295$, F=37.67, df=291, P<0.0001). Just 50% of transect sections had forage and only a weak negative correlation with bear activity (Pearson's r= -0.047). Essentially, signs were randomly distributed in undisturbed forests, but were significantly clustered in post-disturbed and secondary forests, in fragments \leq 10,000 ha, and in areas affected by disturbance. In the few cases where bears occurred in such areas, high sign density/area was likely from *Compression Effects*.

6.9d Site Occupancy Estimates Based On Bear Sign

The distinction between habitat use and actual occupancy is important for both scientific and conservation reasons. For example, a bear can transit through an area and leave signs behind, which can be considered habitat use, albeit minor. However, such incidential use may be minimal or occur only once and could lead observers to spurious assumptions about actual selection and occupancy of that site on a consistent or regular basis.

As noted in Chapter 5, sign detection probability tests indicated good model fit, low variance and habitat bias, and high precision. In terms of whether areas were actually "occupied" by bears on a consistent basis, scale was analytically important. Due to the non-random proximate location of 10 m sub-sections along transects, the detection of signs at this scale of resolution may be a false indication of overall site occupancy. In contrast, as the survey area increased to the 500 or 1,000 m scales, there was a very strong chance that an animal would be detected. At these broad scales, there was a much higher probability that a bear was occupying that area on a consistent basis and any conclusions of site occupancy held less meaning. Further, such large scales included multiple habitat types, but which habitat types were occupied or avoided could not be determined with precision. Estimate precision was best achieved by multiple replicates at the 100 m section level, where habitat character was more uniform and variance in both the probability of detection and site occupancy were lowest.

Asymptotic chi-square quadratic tests in programme CONTRAST of site occupancy probabilities revealed that occupancy rates were significantly higher in undisturbed primary lowland and mid-elevation forests than in all other undisturbed or disturbed habitat types $(X^2 = 2644.57, df = 4, P < 0.00001)$. Figures 6.10 and 6.11 illustrate these differences. Table 6.6 lists site occupancy and detection probabilities for all study areas. Kayan Mentarang National Park was estimated to have the highest site occupancy rates at > 90% with detection probabilities over 94% in the mid-elevation primary forests of the more remote interior (Nnggeng Tau). In Sumatra, the highest site occupancy rates were found in Gunung Leuser National Park in undisturbed primary montane forest > 1,000 m as and primary midelevation forests along the foothills. These areas were estimated to have about 75 - 84%occupancy rates and detection probabilities were 47 - 75%. The lower limits of these rates were probability due to moderate levels of human activity within the areas and habitat disturbance < 3 - 4 km from some sites. This same pattern was observed in primary forests of East Kalimantan (e.g. Lalut Birai, Bahau Primary Forests, Tukuk Mawot), where human activities were more prevalent and habitat disturbance was < 3 - 4 km away. Secondary forests > 20 yrs old had moderate site occupancy and detection probabilities. Although reduced-impact logging (RIL) was practised in primary forests, these post-disturbed forests had lower occupancy and detection probabilities than 20+ year old secondary forests. Conventional logging (CNV) in primary forests resulted in very low occupancy rates, while local clear-cuts, gardens, plantations, and young secondary forests < 10 years old had very low detections and zero site occupancy estimates.



Relative Disturbance

Figure 6.10. The proportion (as means) of sites occupied by sun bears in variously-disturbed habitats based on sign as estimated using the MacKenzie *et al.* (2002) model in programme PRESENCE.



Figure 6.11. Actual site occupancy estimates for sun bears in all sites of variously-disturbed habitats based on sign as estimated using the MacKenzie *et al.* (2002) model in programme PRESENCE. Estimates correspond with table 6.6.

Sun Bear Density and Abundance Results

Site	Habitat	ψ	σ^2	р	σ^2	AIC
Nnggeng Tau	Primary Forest (protected)	1.00	0.0001	0.9444	0.0184	42.62
Alango	Primary Forest (pre-disturbance)	1.00	0.0001	0.8749	0.1618	101.67
Ulu Stee	Primary Forest (protected)	1.00	0.0001	0.8192	0.1037	77.91
South Seturan	Primary Forest (pre-disturbance)	1.00	0.0001	0.7421	0.0317	220.92
Jalungkereng	Primary Forest (protected)	1.00	0.0001	0.7097	0.1520	26.18
Tukuk Mawot	Primary Forest (undisturbed)	1.00	0.0001	0.6545	0.0453	145.81
Gunung Sidih/Loreh	Primary Forest (pre-disturbance)	1.00	0.0001	0.4500	0.0642	88.58
Lalut Birai	Primary Forest (protected)	1.00	0.0001	0.3529	0.1421	206.10
Sei badak	Primary Forest (protected)	0.9935	0.1673	0.6008	0.0396	462.68
Gunung Runtuh	Primary Forest (protected)	0.8348	0.0762	0.4692	0.0355	302.09
Tankahan	Primary Montane < 1200 m asl (protected)	0.7922	0.0829	0.7957	0.0942	281.82
Sekundur	Secondary Forest > 25 years old	0.6296	0.1220	0.2978	0.1443	156.15
Seturan	RIL Primary Forest (post-disturbance)	0.5806	0.1113	0.2368	0.0411	182.80
Alango	Secondary Forest > 20 years old	0.5252	0.1877	0.2618	0.0749	61.79
Bahau Primary Forest	Primary Forest (hunting)	0.3977	0.1665	0.1686	0.0987	67.43
Tukuk Mawot	Primary Forest (hunting)	0.3724	0.0991	0.6749	0.1452	37.93
Tankahan	Primary Montane < 1200 m asl (protected)	0.3354	0.1937	0.3975	0.1114	38.53
South Seturan	CNV logged Primary Forest (post-disturbance)	0.3193	0.1079	0.3626	0.0638	106.43
Bahau Secondary Forest	Secondary Forest < 10 years old	0	0	0.2762	0.0943	80.39
Gunung Sidih/Loreh	CNV logged Primary Forest (post-disturbance)	0	0	0.2219	0.1275	74.49
Alango	Garden (post disturbance)	0	0	0.0055	0.1976	75.42
Aras Napal	Plantation and Gardens	0	0	0.0042	0.0025	29.91

Table 6.6. Actual site occupancy (ψ) and detection probabilities (*p*) of sun bears in all study sites as estimated using the sign data in the MacKenzie *et al.* (2002) model in programme PRESENCE.

6.9e Site Occupancy Estimates Based on Camera-Trapping

Although identification rates of sun bears were as high as 70% in East Kalimantan, camera angles, body positions, lighting, and so forth limited 100% positive identification of every photo-captured bear. Consequently, traditional capture-recapture modelling was not possible, but photos were firm evidence of bear presence in an area. These data were modelled as presence-absence data in programme PRESENCE following MacKenzie *et al* (2002), producing detection probabilities, *p*, and site occupancy rates, ψ , which were used to generate bear density estimates *(see* section 6.10b on Bear Density). Camera-trapping results validated sign surveys and showed the same occupancy estimate pattern, where the highest occupancy and detection probabilities were in the most remote undisturbed primary forests.

Northern Sumatra: Estimated site occupancies by camera-trapping ranged from 0 - 100% in the Leuser Ecosystem, with the highest detection probabilities (92%) and occupancy rates (100%) found in the more remote east slope (Sei Birah) and foothills (Sei Badak) of Gunung Leuser National Park. Secondary forests of all ages did not produce any bear photos, thereby reducing the overall occupancy probability for forested areas of the Leuser Ecosystem to 0.3458 ($\sigma^2 = 0.0057$). In this case, the survey-specific model with heterogeneous detections of one group produced the best model fit (AIC=427.78). In order to produce a more accurate estimate of the Leuser Ecosystem, it was necessary to include cleared areas, plantations, and so forth, in the model. Although camera-trapping did not produce photos of bears in these areas, sign surveys did indicate minor and transient use. Thus, sign presence-absence data of these sites were included in a second model. Again, the survey-specific model with heterogeneous detections of one group produced the best model fit (AIC=467.23). The result was a slight reduction in the overall proportion of occupied sites to 0.3005 ($\sigma^2 = 0.0044$).

East Kalimantan: The highest estimated proportion of occupied sites by camera trapping in East Kalimantan was two times higher than in northern Sumatra, estimated at 0.6155 ($\sigma^2 = 0.0193$) in the Ulu Nnggeng interior of Kayan Mentarang N.P. *via* the single season constant detection (*p*) model. This site also had a three-fold higher rate of distinct bear photo-capture events than other study sites in East Kalimantan. Although the survey-specific heterogeneous detection model of one group produced a slightly better fit (AIC=174.09) the constant detection model of one group (AIC=181.38) resulted in the least variance. Regardless, this estimate had relatively high variance compared with other sites. This same model was the best fit (AIC=152.18) of the camera data for the Bulungan Research Forest near Seturan, but with a lower occupancy rate (ψ =0.3648) and variance (σ^2 =0.0129). In the

BRF, the proportion of sites occupied was highest in undisturbed primary forest, with almost double the number distinct bear photo-capture events (n=14) than other habitats (n=8).

6.10 Sun Bear Density and Abundance

6.10a Range Overlap

Because bears could not be identified by photographs with 100% accuracy, rangeoverlap estimates were not possible with photo data. Based on genetic samples, the minimum distance between identified bears in the Kayan Mentarang National Park study site was 1,500 m in aerial extent as mesured by GPS coordinates. This does not suggest an absence of overlap. Indeed, Wong (2002) found that overlap among sun bears in Sabah ranged from 0.54 to 3.45 km². The genetic samples from the present study can only indicate that the bears in this site were present within at least 1,500 m of each other. In this case, two bears were on the same side of a major river confluence (Sungai Nnggeng, Sungai Stee, and Sungai Jalungkereng) and there were no major geographic barriers between the two samples. These two genetic samples, however, were geographically separated from the other samples by several more river arteries and confluences, multiple ridge lines increasing in both elevation (> 500 m) and steepness (> 90°), and 2 – 10 km in distance. The maximum distance between genetic samples of identified individuals was 9.1 aerial km.

6.10b Population Density and Abundance

Estimates reported below are based on camera-trap data in the best-fitting siteoccupancy models according to AIC and variance results (section 6.9e). This method retains promise and is based on empirically-based presence-absence data, theory (MacKenzie *et al.* 2002, Royle and Nichols 2003), and home ranges, but it relies on assumptions in the models and in home range estimates of sun bears (n=4) from another study and site on Borneo by Wong (2002). The latter estimates were by VHF telemetry and minimum convex polygon (MCP) methods that have inherent error and assumptions. It is stressed that results are not absolute figures. These are estimates, with hypothetical demographic scenarios based on the literature, meant as baselines for future studies. Validation of this method for sun bears is needed by other proven means, such as mark-recapture with 100% individual identifications.

Spacing among individuals of some species (including bears) is potentially densitydependent, depending on habitat, forage, demographics, and environment. Thus, home ranges may vary. Given the assumptions of the MacKenzie *et al.* (2002, 2003) and Royle and Nichols (2003) models, along with those in sun bear home range calculations (n=5) by Wong Chapter 6

(2002), several density estimates were calculated (table 6.7) using camera site occupancy (ψ) results. Camera plot-level analyses with multiple replicates (n=7–9 sample occasions) at 24–32 plots per 48–64 km² survey area produced the most robust models with least variance and satisfied independence assumptions for estimated sun bear home ranges (4–20.6 km²).

Region	Study Site	W	Home Range (Wong 2002)	6.2 km ²	(mean) 14.8 km ²	15.56 km ²	16.8 km ²	20.6 km ²
	(km ²)		Density D / km ²	D	D	D	D	D
Gunung Leuser National Park	384	0.3458		0.0558	0.0234	0.0222	0.0206	0.0168
Leuser Ecosystem	414	0.3005		0.0485	0.0203	0.0190	0.0178	0.0146
Bulungan Reseach Forest	96	0.3648		0.0588	0.0246	0.0234	0.0217	0.0177
Kayan Mentarang National Park	96	0.6155		0.099	0.0416	0.0395	0.0366	0.0299

Table 6.7. Sun bear density estimates for the three main focal areas using all home range estimates for four male sun bears in Sabah as estimated by Wong (2002).

As expected, resulting densities were relatively similar in the mid-ranges, whereas they were noticeably contrasting at the two extremes, such that small ranges may suggest higher densities and *vice-versa*. This assumption depends on the area of available habitat and, thus, population abundance may not correspond with high densities. In small patches, density-dependent spacing may compress bears into remaining suitable habitat, resulting in what appears like higher densities, but of fewer individuals, whereas in large contiguous forests bears are more dispersed. Thus, the known mean sun bear home range (14.8 km² ± 6.1 SD) (Wong 2002), which coincides well with closet kin, was used to test the models for a range of possible sun bear abundance estimates. The following estimates include three hypothetical demographic scenarios based on literature to account for bear overlap variance. Table 6.8 lists population estimates under each scenario (N_b , N_z , N_s) for each focal main area.

- (1) N_t , Adult bears only. This is a minimum estimate based on a home range of 14.8 km² (± 6.1 SD) and one adult bear/range with no range overlap among bears.
- (2) N_2 , 50% overlap. Wong's (2002) telemetry study in Sabah showed that four male sun bears had a mean home range of 14.8 km² with overlap of 3.2 – 22.2%. Several assumptions were considered for abundance estimates: (a) female Ursidae offspring will occasionally overlap with their mothers, (b) male Ursidae are typically more territorial than females, (c) male Ursidae will usually include at least 1 – 2 females within their home range, and (d) a 50:50 sex ratio. Although < 20% mean home range overlap is more common for Ursidae, some bears (particularly female offspring with their mothers) have higher overlap. Thus, an estimate using a liberal overlap of 50% was calculated for possible range overlaping and unobserved bears.

(3) N_3 , 1 male + 1 female + 1 cub/female. It is known through zoo studies that one female can produce an average of 1 - 2 cubs every 2 - 3 years. Based on other Ursid studies, there is ca. 50% cub survival to reproductive age in the wild among the sun bear's closest kin. Thus, an estimate was calculated based on one male per female accompanied by one cub, thereby tripling the original N_1 estimate.

Northern Sumatra: In Gunung Leuser National Park the best-fitting (AIC=427.78) model (single season, survey-specific *p* with heterogeneous detections) with the least variance ($\sigma^2 = 0.0057$) had a site-occupancy estimate of $\psi = 0.3458$ for undisturbed primary forest and 20+ year-old secondary forests. Combined with Wong's (2002) mean home range (14.8 km²) and no range overlap this would indicate *D*=0.0234 bears/km⁻². Thus, if the entire ecosystem (24,000 km²) consisted *only* of these forest types, a population estimate for the ecosystem would be ca. 561 adult bears (± 122.43 SE). But, there were no bear camera captures in secondary forests younger than 20 years old, nor in disturbed areas inside or bordering the park, both of which occur in large portions of the ecosystem. Thus, table 6.8 shows that, *only* for the protected areas of Gunung Leuser National Park (8,000 km²) and scenario N₂ of 50% range overlap, the best AIC-fitting site-occupancy model and mean home range produces N=280.4 \pm SE 61.2 sun bears at D=0.035 bears/km⁻². By comparison, the best AIC-fitting abundance-induced model (AIC=711.60) was the Repeated Count model (Royle and Nichols 2003) with an actual estimate of N=258.93 \pm SE 14.27 sun bears (95% CI=230.96 – 286.90) at a density of 0.032 bears/km⁻².

Table 6.8. Sun bear population estimates for the three main focal areas based on the mean home range estimate (14.8 km²) by Wong (2002) and site-occupancy modelling from this study. $\psi =$ proportion of area occupied as estimated by programme PRESENCE; D = density of bears/km⁻²; $N_i =$ min. population estimate of adults with no overlap; $N_2 =$ population estimate of adults only with 50% range overlap; $N_3 =$ population estimate of one male per female with accompanying cub.

Region	Study Site (km ²)	Effective Available Habitat (km²)	Ψ	D / km ⁻²	N _I (min) adults (no overlap)	N ₂ adults (50% overlap)	<i>N</i> ₃ adults + 1 cub / ♀	SE (N ₁) (±)
Gunung Leuser National Park	384	8,000	0.3458	0.0234- 0.0702	186.9	280.4	560.7	40.8
Leuser Ecosystem	414	18,350	0.3005	0.0203- 0.1397	372.6	558.9	1,117.8	82.24
Bulungan Research Forest	96	4,226	0.3648	0.0246- 0.0739	104.2	156.3	312.5	32.43
Kayan Mentarang N.P.	96	14,000	0.6155	0.0416- 0.1247	582.2	873.3	1,746.7	131.4

Because a minimal amount of signs were observed along 65 km of transects in some disturbed areas of Leuser, it can be assumed that bears will occasionally use or transit through these sites. Thus, I modelled these data with the camera data and the best-fitting occupancy estimate ψ =0.3005 (σ^2 =0.0044) decreased the density to 0.0203 bears/km⁻² for

the overall ecosystem. Assuming this survey combination of minimally-disturbed forests and disturbed areas represents an approximate geographic proportion (~ 93% forests : 7% disturbed areas) of habitat types across the ecosystem, it would lower the total ecosystem population estimate to about 373 adult bears (\pm 82.24 SE). The latter estimate accounts for ca. 565,000 ha of primary forest that were lost between 1985 and 2000 (LMU unpub. data), reducing the effective-available forested habitat in the ecosystem to 18,350 km².

East Kalimantan: Bear densities in the Bulungan Ecosystem were comparable to Leuser. The site occupancy model for Bulungan (single season, constant *p*) with the best fit (AIC=152.18) and least variance ($\sigma^2 = 0.0129$) in minimally-disturbed primary forests was $\psi=0.3648$. With $\psi=0.3648$ and a mean home range of 14.8 km², *D*=0.0246 bears/km⁻². A population estimate for the greater Bulungan Research Forest (4,226 km²) would be ca. N=156 adult bears (± 48.64 SE) for scenario N₂. Kayan Mentarang N.P. and adjacent forests had the highest density of bears in all of the study areas. The proportion of sites occupied ($\psi = 0.6155$, $\sigma^2 = 0.0193$) *via* the single season constant detection (*p*) model (AIC=181.38) was > 61%. Using $\psi=0.6155$ and mean home range (14.8 km²), *D*=0.0416 bears/km⁻². Given Kayan Mentarang N.P. (14,000 km²) is mostly forested, most of which is available to bears, a possible estimate would be ca. N=873 adult bears (± 197.1 SE) for scenario N₂.

6.11 Sun Bear Population Distribution

At a landscape scale bears in these study areas have clumped distribution. Chisquare tests of sign distribution at the micro-habitat level indicated sun bear signs were clustered in disturbed sites and, while signs were randomly distributed <u>within</u> primary forests patches, 87.5% of bear signs were clustered between occupied primary forest patches at the landscape scale ($X^2=19.75 - 138.28$, df=3 - 39, P<0.0002). Photographic captures indicated the same pattern. The preponderance of these analyses show a common and significant trend across all study sites, ecosystems, and regions: that being, sun bear use of disturbed and nonforested areas, young secondary forests, edges, agricultural areas, clear-cuts, and so forth was insignificant relative to the overall population and landscape use.

Results demonstrated clearly that the distribution of sun bear habitat use among occupied sites *across* the landscape is fragmented. Both sign and camera-trapping results reveal that sun bears are randomly distributed within undisturbed primary forests, but are clustered between occupied sites and "compressed" in sites affected by disturbance. Consistently occupied sun bear habitat is mainly in undisturbed primary forest at elevations between 400 – 1,000 m asl. Some bears used older secondary forest (>20 – 30 years old), but this is statistically insignificant relative to the overall population and its landscape use.

6.12 Efficacy of Methods

6.12a Tests with Tiger Data

In collaboration with the Leuser Management Unit, all camera-trapping for this sun bear research in Leuser was designed to estimate population densities, distributions, and habitat use of both sun bears and Sumatran tigers *(Panthera tigris sumatrae)*. Tigers were a good species to test these methods because individuals could be positively identified. Both tigers and bears were the target species at all trap sites during the same surveys in Leuser, such that dual cameras were set-up to identify tigers by their stripe patterns (figure 6.12) while also trapping all other species, including bears. Every trap was set-up using consistent protocols, regardless of habitat type or species, and the same stratified-random design was used as in sign surveys. No baits were used in order to trap all species without bias.



Figure 6.12. Remote photo of adult male Sumatran tiger (*Panthera tigris sumatrae*) identified as "Zoro". Photo was taken at 15:30 on 23 March 2002 at the Durian Cinguk trap site (210 m asl) in the Sei Badak area of Gunung Leuser National Park (© 2002 LMU & Dave Augeri).

There were a total of n=9 independent tiger captures, from which 6 tigers were positively identified. Two other tigers were unidentified, which could have been different tigers or any of the other six. Thus, the minimum number of individuals in the 384 km² study area was 6 tigers. This minimum number of individuals with defined territories suggests a density of 1.56 tigers/100 km² (\pm 0.63 SE), which is consistent with the most recent estimate for tigers in southern Sumatra, 1.6 – 1.7 tigers/100 km² (O'Brien *et al.* 2003). If the other two unidentified tigers are different individuals, the density would be 2.1 tigers/100 km².

Tiger camera-trapping results validated methods used for bears when modelled as presence-absence data in PRESENCE. Survey-area level (64 km²) analyses (n=6) with multiple replication of 8-9 sampling occaisons at 32 trap sites in each 64 km² survey area provided the most robust models and satisfied potential independence assumptions given the tiger's large ranging patterns (> 50 km² in Sumatra). But, it is emphasised that n=9 unique

captures raises possible sample size and model assumption issues. The single-season and multi-season site-occupancy models had the same site-occupancy ψ =0.7697 and detection probability *p*=0.5197 for tiger presence-absence camera data. But, the multi-season model of seasonal occupancy and colonization fit best (AIC=31.08) with least variance (σ^2 =0.0199).

With a minimum n=6–8 tigers/384 km², a mean home range for this territorial species in Leuser could be ca. $48 - 64 \text{ km}^2/\text{tiger}$. O'Brien *et al.* (2003) estimated a total of 40 – 43 adult tigers in southern Sumatra in an area with effective available habitat of 2,569 km² (3,568 km² total area minus habitat loss of 28%), suggesting a mean home range of ca. 59.7 – 64.2 km²/tiger. The Sumatran Tiger Project recently estimated a tiger home range in central Sumatra of ca. 50 km² over two months (D. Priatna pers. comm.). Thus, using an average home range of ca. 57 km² for the region and the best estimated tiger site-occupancy rate (ψ =0.7697) from presence-absence data, the density would be *D*=1.35 tigers/100 km² for this study area. This density is similar to our camera-trapping and modelling results of positively-identified tigers and those in southern Sumatra estimated by O'Brien *et al.* (2003) (table 6.9).

By using camera data in the best occupancy model and the possible mean tiger home range (57 km²) for the region, this method suggests a population estimate for Gunung Leuser National Park (8,000 km²) could be N=108 adult tigers (SE \pm 20). By comparison, the Abundance-Induced Heterogeneity model (Royle and Nichols 2003) (AIC=54.97) estimated N=123 tigers (SE \pm 79) and the minimum number of camera-captured tigers positively identified from this study (n=6 – 8) indicates N=125 – 167 tigers (SE \pm 50) in the Park.

Table 6.9. Comparisons of tiger densities and abundances using presence-absence modelling and positive ID by camera-trapping in this study in Gunung Leuser National Park and by positive ID from camera-trapping in Bukit Barisan Selatan National Park, Sumatra by O'Brien *et al.* (2003). Standard error (SE) for camera-trapping estimates of identified tigers in Gunung Leuser was estimated by the following equation, where $\hat{p} = \text{density/km}^2$ and n = sample area units (Ott and Longnecker 2001): $SE = \sqrt{\frac{\hat{p}(1-\hat{p})}{n}}$

Tiger Population Estimate Methods	Site	Sample Area (km ²)	Total Identified Tigers	ψ	Density (km ⁻²)	SE (D) (±)	Ñ	SE (\hat{N}) (±)
Site-Occupancy multi-season model	Gunung Leuser	384		0.7697	0.0135	0.0025	5.25	0.95
Abundance-Induced Heterogenity model	Gunung Leuser	384		0.7834	0.0153	0.95	6.12	3.82
Postive ID Capture-Recapture	Gunung Leuser	384	6 – 8		0.0156 - 0.021	0.0063	6-8.1	2.43
Capture model (M _{bh})	Gunung Leuser	384	6 – 8		0.0156	0.0063	6	0.504
Mark-Huggins model (M _b)	Gunung Leuser	384	6 – 8		0.0163	0.0065	6.27	0.746
O'Brien <i>et al.</i> (2003) model (M _h)	Bukit Barisan	836	9		0.016 - 0.017		13	3.66
6.12b Sign-Surveys and Camera-Trapping

Animal signs can appear as though they were generated by more than one individual, thereby producing high detection and site occupancy probabilities, whereas camera trapping detects particular individuals in the current time of occupancy. When comparing the estimated proportion of area occupied by bears (ψ) between sign surveys and camera-trapping, results reflected inherent differences between these two methods. Importantly for this comparison, sign survey data were restricted to signs produced within the same site and year as camera data. Variances calculated for each model in programme PRESENCE were averaged and used to generate a range of mean estimated ψ values for each site (table 6.10).

As expected, results demonstrated that the sign survey site occupancy probabilities and associated variances were higher than for camera trapping in the majority of cases. The one exception was in the Bulungan Research Forest (BRF), where the mean sign site occupancy probability was slightly lower than estimated by camera-trapping. Low photocaptures in the BRF reflect correspondingly lower sign abundances in some areas and *viceversa* in other areas, but the estimated ψ value ranges overlapped (table 6.10), suggesting no significant difference. There was not ψ value range overlap in the Leuser Ecosystem, but the chi-square tests were not significant between the two methods (table 6.10).

All occupancy probabilities and associated variances were then compared between sign surveys and camera-trapping within each site using the asymptotic quadratic chi-square test (Sauer and Williams 1989) in programme CONTRAST. Tests resulted in no significant differences between occupancy probabilities produced by the different methods within the sites (table 6.10).

Table 6.10. Comparisons of occupancy probabilities (ψ) between sign surveys and camera-trapping within the three main focal areas, which also represent higher (Leuser), medium (Bulungan), and lower (Kayan Mentarang) levels of disturbances. Value ranges between sign surveys and camera trapping overlap within the East Kalimantan sites. Asymptotic quadratic chi-square tests resulted in no significant differences between actual ψ values within each site.

Site	Asymptotic X ² Test	Si	gn Survey	Camera Trapping		
		$Mean \ \psi$	Mean ψ Range	$Mean \ \psi$	Mean ψ Range	
Leuser Ecosystem	X ² =8.9641, df=5, P=0.1105	0.5122	0.4204 - 0.6025	0.3005	0.2961 - 0.3049	
Bulungan Research Forest	X ² =3.907, df=3, P=0.2715	0.3181	0.1856 - 0.3976	0.3648	0.3519 - 0.3777	
Kayan Mentarang Ecosystem	X ² =4.4451, df=7, P=0.7273	0.6153	0.5711 - 0.6596	0.6155	0.4766 - 0.7544	

6.12c Genetic Samples and Camera-Trapping

The majority (58%) of usable genetic samples, 75% of genetically identifiable individuals, and 36% of distinct sun bear photo events in Kayan Mentarang were all recorded at one study site, the Jalungkereng area. Based on genetic sampling the following correlations with camera-trapping analyses were considered.

Four different genetically-identifiable bears were recorded in the same 96 km² grid that was used for camera-trapping and sign surveys in Kayan Mentarang National Park and border areas. The genetic samples were found within six months of camera-trapping. With no overlapping home ranges, this minimum number of positively-identified bears would produce a density D=0.0417 bears/km⁻² (± 0.0204 SE). Standard error (SE) was calculated by the same equation used for tigers identified by camera-trapping (table 6.9). This density is very close to D=0.0416 bears/km⁻² for the same study site estimated by site-occupancy camera-trap models (table 6.8) with Wong's (2002) mean home range 14.8 km² (± 6.1 SD).

Using genetic identification and assuming (a) n=4 is the minimum number of bears in the study area, (b) 50:50 sex ratio, and (c) 50% adult range overlap or 1 cub per female, it would potentially add approximately 2 more bears to the 96 km² site for a minimum of 6 individuals at a density D=0.0625 (± 0.0247 SE) bears/km⁻². Hence, based on genetic sampling, a density of 0.0417 – 0.0625 bears/ km⁻² suggests a population estimate of ca. 584 – 875 bears (± 285.63 – 345.8 SE) in the 14,000 km² area of Kayan Mentarang N.P. This estimate is similar to the N_1 and N_2 estimates (582 - 873 bears) in table 6.8 using the cameratrapping site-occupancy models. Reversing the process to estimate home range suggests that 4 - 6 bears with no overlap in the 96 km² study area have a mean home range of ca. 16 - 24km², which is within the extent of Wong's (2002) telemetry results for four adult male bears with ranges between ca. 6 - 20 km² and estimated range overlaps of 3.2 - 22.17%.

The above genetically-based estimates do not account for recapture rates, which were inferred from the following camera-trapping results. A total of 2,688 trap nights were needed to produce 29 independent photo events of sun bears in the Kayan Mentarang study area. Wong *et al.* (2004) recorded 46 separate photo events of four male sun bears identified by telemetry in the Danum Valley, Sabah. In the latter study, 858 trap nights were conducted and produced recaptures of 3 marked bears 31 times, with a mean of 10 photos/individual. Considering Wong's photo recapture rate of 67% of known individuals and assuming that the remaining 33% of Wong's captures consisted of new individuals at the same capture rate of 67%, this would add ca. 1 - 2 more bears to Wong's sample population. In the current study, three times more trap nights were required to produce 37% fewer photo events in Kayan Mentarang than in the Danum Valley study, which would possibly suggest a more dispersed

population in Kayan Mentarang. Nevertheless, assuming a recapture rate of 67% of four genetically-identifiable bears with 33% additional bears, this would add 1.32 more bears to this study site population for a total of 5.32 bears. This would indicate D=0.055 bears/km⁻² without range overlap in the study site. With 50% range overlap or 1 cub/female and given a 50:50 sex ratio, the sample population could be potentially 8 bears at a density D=0.083 (± 0.0281 SE) bears/km⁻². Thus, based on genetic sampling and a 67% recapture rate, a possible population estimate for Kayan Mentarang National Park could range between 588 – 1,162 bears (± 286.57 – 394.29 SE), which is within the range of estimates produced by the camera data using site-occupancy models and a mean home range of 14.8 km² (table 6.8).

Table 6.11 lists alternative density and population estimates of camera-trapping and genetic sampling of bears with a liberal 50% overlap in Kayan Mentarang National Park. This comparison shows that the estimates between the two methods are similar. Figure 6.13 provides a similar comparison when examined only with adults with no range overlap. It is important to emphasise that Wong had a 66.6% loss of telemetry captured individuals, half of which were known mortalities. Thus, without other influences, such as forage crop failures, hunting, and so forth, cub recruitment may simply be replacing adult mortalities.

Table 6.11. Comparison between camera data site-occupancy model results and genetic analyses for density (*D*), population (*N*), and study site (*n*) estimates of sun bears in Kayan Mentarang National Park for 4 scenarios (A-D) with liberal 50% bear range overlap. The study site is 96 km². Home ranges 6.2, 15.56, 16.8, 20.6, 14.8 (mean) km² were estimated by Wong (2002). Home ranges 12, 16, 19.2, 24, 17.5 (mean) km² were estimated from densities in the study site by the minimum number of genetically-identified individuals.

Method	Parameter	Scenarios				Mean	± SE				
		А	В	С	D		-51				
Camera Trapping	Actual Home Range (km ²)	6.2	15.56	16.8	20.6	14.8	3.05				
	D / km^{-2}	0.0993	0.0395	0.0366	0.0299	0.0416	0.0094				
	<i>n /</i> 96 km ²	14.26	5.7	5.25	4.5	5.9	2.3				
	<i>N</i> / 14,000 km ²	2084.7	829.5	768.6	627.9	873.3	197.1				
	% Range Overlap for <i>n</i> and N	50	50	50	50	50	50				
Genetic Sampling	Estimated Home Range (km ²)	12	16	18	24	17.5	2.5				
	D / km^{-2}	0.0833	0.0625	0.0554	0.0417	0.0607	0.0087				
	<i>n /</i> 96 km ²	8	6	5	4 (pos. ID)	5.75	0.85				
	<i>N</i> / 14,000 km ²	1,166.2	875	775.6	583.8	850.2	121.4				
	% Range Overlap for <i>n</i> and N	50	50	50	0	50	50				



Figure 6.13. Graphic comparison between camera trapping and genetic sampling density (D) and minimum population (N_l) estimates of only adult bears without range overlap in Kayan Mentarang National Park.

6.12d Correlations Between Genetic Samples and Sign-Surveys

The majority (58%) of usable genetic samples in Kayan Mentarang were found in one area, the Jalungkereng study site, and 75% of these were within 2,105 m of each other. The highest frequency (n=92) of bear signs/ha and the second highest mean density of bear signs/ha across all 16 study sites on Borneo and Sumatra were also recorded in Jalungkereng.

Given the Jalungkereng area is at the confluence of 3 upland river drainage systems, it is possible that this ecotone attracted overlapping ranges of ≥ 2 bears. In addition, the area consists of numerous valleys and ridges rising in elevation to the north and west. Consequently, the landscape configuration is geographically narrow, which may potentially funnel or restrict animal movements in the area. Demographic data also showed that bears in the Jalungkereng area belonged to smaller size classes. Thus, it is possible that this area's ecological attraction and geographically narrow position between the less productive, more disturbed Lalut Birai lowlands, and the protected western interior is compressing some bears between **a**) a dense and protected bear population composed of larger and perhaps more dominant individuals in the western interior and **b**) moderate to high levels of human activity in the less productive eastern lowlands.

The high number of genetic samples and dense sun bear signs produced at this site appear to be correlated. Given that a majority of genetic samples and identifiable individuals occurred in the Jalungkereng area with correspondingly-high sign density and moderate levels of distinct photo events, the likelihood of this correlation is reasonable. CHAPTER 7

DISCUSSION



"Who can explain why one species ranges widely and is very numerous, and why another allied species has a narrow range and is rare? Yet, these relations are of the highest importance, for they determine the present welfare, and, as I believe, the future success and modification of every inhabitant of this world."

Charles Darwin, The Origin of Species (1859)

DISCUSSION

7.1 Introduction

Explaining the true nature of ecological dynamics requires acute understanding of the movement and location of individuals and populations in space and time relative to each other and their environment. The synergism among movement patterns, ecological processes, and the non-linear effects of landscape structure drives population dynamics, substantially affecting the probability of survival or extinction of sub-populations (Wiens 1997, Hanski and Gilpin 1997).

Ecological processes are ephemeral (Thrall *et al.* 2000), especially at a local level, but species persistence depends on the degree to which increased isolation and loss of suitable habitat affect within-patch dynamics and between-patch processes, such as dispersal, colonisation, and gene exchange. Results supported the theoretical framework outlined in Chapter 3 and revealed possible insular, risk (relative to both the cost:benefit of foraging decisions and disturbance), and stress-related effects on sun bear movements and habitat use across all sites and ecosystems.

Bear behaviours, movements, and persistence are influenced by food, environment, biogeographic condition, health, and cover. The diversity, structure, and security of primary forests are important for many species and this remained true for sun bears in these sites. The original *a priori* objective of this work was to examine multiple parameters that could potentially influence sun bear landscape use. Yet, the preponderance of results indicated that disturbance was consistently the most dominant effect. Tests revealed that habitat disturbance was the most significant and dominant interactive influence on sun bear habitat use, including when disturbance was within 5 km of bear activity in primary forest. The significant majority of sun bear activity was observed in higher degrees of cover and security in primary forests and the most dominant habitat traits associated with 97% of all observed bear activity were strongly associated with a diverse and maturely-structured undisturbed forest community, regardless of the ecosystem.

In addition, despite thousands of hours of effort with extensive geographic coverage in diverse habitat types and conditions across multiple ecosystems, no photographs or genetic samples were recorded in secondary forests of any age, or in CNV-logged forests, agricultural areas, roads, edge habitats, or other disturbed areas. Essentially, as the level, intensity, and extent of disturbance increased across sites, significantly less bear activity was observed.

7.2 Efficacy of Methods

Prior to conclusive interpretations, it is important to examine whether the methods used produced valid results. The study of ecological patterns and variation is not exact and some inference is required. The practical limitations of this study were minimised through quantification and redundancy and applying a stratified-random sampling design minimised independence violations and improved generalisation across sites beyond potential habitat bias, individual variation or other possible prejudices. Importantly, theoretical assumptions applied in the models and methods used did not appear to be violated and withstood practical application. Because no animal or species lives in a vacuum and is subject to multiple influences, perhaps the most important aspects regarding the validity of these results were:

- (1) Stratifed-random sampling with a large number of independent random samples in multiple habitats, ecosystems, regions, seasons, and years, which reduced habitat bias and individual variation, enabling more confident generalisations across sites.
- (2) Method testing, plurality and redundancy, as well as simultaneous sampling in different sites, thereby reducing methodological, site, and time biases.
- (3) A nested experimental design, which reduced statistical bias, violations of independence, and other confounding effects.
- (4) Tested habitat bias and sign aging, particularly relative to disturbance, human activity, and other factors like the presence of influential sympatric species, which reduced misleading extrapolations.
- (5) Extensive statistical modelling of multiple potential effects and their interactions, which reduced spurious conclusions of arbitrary effects.

In terms of bear density and abundance estimates, some assumptions exist in the models and this integrated method along with possible problems of applicability and error in home range estimates of a small sample of sun bears (n=4) from another study and site on Borneo by Wong (2002), who used conventional telemetry and methods with inherent assumptions (*see* Chapter 6). Tests in the current study show the data and models in the present analyses were robust and ecologically realistic, but the density and population figures should be interpreted cautiously as estimates with associated error and assumptions.

On a practical level, sign surveys did not provide absolute density and abundance estimates, but reflected relative differences in the intensity and amount of use and occupancy among specific areas. When considered relative to camera-trapping and genetic sampling across multiple sites, habitats, and biogeographic conditions, the same pattern emerged across more than 50 different habitat types and conditions in all 16 study sites, 6 focal areas, 3 regional ecosystems, and 2 islands. That being, in areas with high bear sign frequencies,

there were more independent photo events, higher estimated site occupancy and detection probabilities, and more genetically-distinct samples. Where there were significantly fewer bear signs there were correspondingly less photo captures and genetic samples.

7.2a Tests of Camera-Trapping vs. Sign-Surveys

Camera-trapping data of tigers enabled useful tests of method efficacy. Using the same methods on a more elusive species with a larger range like the Sumatran tiger, which could be positively identified in the same sites during the same periods, provided a good comparative test of the models and methods. It must be noted that there were only n=9 independent tiger capture events, which raises potential sample size issues and some model assumptions. Nevertheless, when analysed in the same presence-absence models as bears, the tiger models validated both the camera and sign-survey methods used on bears. As presence-absence data and models, estimated tiger densities were very close to the results produced by both conventional capture-recapture models and photo identification and were also very close to estimates in southern Sumatra provided by O'Brien *et al.* (2003).

The apparent distinction between sign-survey and camera-trapping site-occupancy estimates is important. Essentially, one bear can produce a large amount of signs that can last for years in any particular area. Such signs can appear generated by more than one individual, thereby producing high overall detection and site-occupancy probabilities that may or may not be consistent with the present time. In contrast, camera-trapping detects the presence of individuals by independent events (e.g. sightings) in the current time of occupancy. Sign-surveys show higher detections and site occupancy probabilities, whereas camera-trapping produces more precise and realistic site-occupancy estimates based on real-time detections. When comparing the estimated proportion of area occupied (ψ) by bears between sign-surveys and camera-trapping, the results reflected these relative differences. Sign-survey occupancy probabilities were higher than for camera-trapping in the majority of cases, but the estimated ψ value ranges overlapped and tests were insignificant between occupancy probabilities produced by the different methods within the sites.

7.2b Tests of Genetic-Sampling vs. Sign and Camera-Trapping Surveys

Genetic sample size was low, but sufficient in one site in Kayan Mentarang National Park to contrast with other methods. Comparisons with camera-trapping demonstrated that the density and population estimates obtained by the two methods were similar. When reversing the calculations to derive home range estimates, results were accurate and fell within published sun bear home range estimates based on telemetry study in Sabah by Wong (2002). Thus, relative to these data this comparison was sound. Given the low genetic sample size, it was not possible to produce rigorous correlative analyses relative to sign censuses, but a few inferences can be made. In the Kayan Mentarang ecosystem the majority of usable genetic samples were found within about 2 km of each other in the Jalungkereng area. The highest frequency of bear signs/ha were also recorded in the same area, along with the second highest mean density of bear signs/ha across all 16 study sites and 36% of the photo captures in Kayan Mentarang.

At a landscape level, this area is an ecotone with moderate levels of bear forage abundance and diversity at the confluence of three upland river drainage systems. The area is a relatively narrow watershed falling between the more protected interior to the west (the "Hulu") and the rich lowlands (Lalut Birai) bordering the primary drainage of the Bahau River to the east. Moderate to high levels of human activity in the form of hunting-gathering, river traffic, local agriculture, villages, and ecological research/monitoring influence the eastern lowland areas of Lalut Birai and the Bahau River. Correspondingly low bear sign densities and photo captures were recorded in those areas. In contrast, the second highest density of bear signs/ha and more than one third of independent sun bear photo events for Kayan Mentarang occurred in the Jalungkereng site > 3.5 km from human activity and disturbance. The remaining 64% of photo events, as well as 42% of usable genetic samples in Kayan Mentarang, were recorded to the highest density and most heterogeneously-dispersed bear signs in all of the Bornean and Sumatran study sites. Demographic data also revealed bears were larger in the latter areas than in Jalungkereng and Lalut Birai.

Given that (a) Ursidae are not strictly territorial and will occasionally overlap, (b) published sun bear home ranges on Borneo are $4 - 20.6 \text{ km}^2$ with 3.2 - 22.17% overlap (Wong 2002, Normua *et al.* 2003, 2004, Meijaard *et al.* 2005), (c) published daily ranges on Borneo have been observed up to 5,660 m (Wong 2002), and (d) the relatively high sign density found at this site, it is possible that the genetic samples in the Jalungkereng area correlated with potential bear overlap and relatively high density in that area, where the ecotone attracted overlapping ranges of bears. Demographic and disturbance data, however, suggest that it is equally likely that this area is compressing smaller or subordinate bears between a relatively dense and protected bear population in the western interior, composed of more dominant individuals, and moderate to high levels of human activity in the disturbed eastern lowlands.

7.2c Conclusions on the Efficacy of Study Methods

Analyses indicated that the stratified-random study design, large number of independent surveys in multiple habitats and sites, and plural methods overlaid in the same

sites during the same and different periods, together accounted for an appropriate degree of individual variation and habitat bias. These results provided assurance that the methods and models used in this study were robust and ecologically realistic, but should be generalised only across these study sites. There was a positive correspondence among sun bear sign frequencies, photo captures, and genetic samples and it can be concluded that, when signs are properly aged, sign abundance and distribution were an appropriate index of the relative degree of sun bear habitat use. The preponderance of these analyses show that (1) sign absence likely indicated bear avoidance of those areas and (2) moderate bear activity was either selection or exploration of specific sites. Overall, results revealed a strong common pattern across all study sites and demonstrated that the dynamic geometry of landscape structure and disturbance can influence bear ecology on Sumatra and Borneo.

7.3 Biogeography

Biogeographic conditions are important influences on animal movement and habitat use. More than 20 habitat, topographic, and biological variables in this study were tested as effects on sun bear geographic ecology. Topography affects forage type, diversity, and abundance as well as the degree to which individuals can access resources and compete with or prey on other species. This can occur directly by landscape features (e.g. steep terrain, canyons or narrow watersheds, and so forth) that either facilitate or limit access to suitable habitats, and/or by directly affecting the productivity of habitats through, for example, elevation, slope and aspect. In undisturbed sites, slope and aspect variation were not significant effects on sun bear habitat use, but elevation was important, where the highest sign, photo, and genetic sample frequencies were in undisturbed mid-elevation primary forests (450 - 1,000 m asl). But, at all elevations, significantly more bear activity was associated with older more heterogeneous primary forest traits, such as high canopy cover (>95%) and refugia (> level 3), low ground cover (<20%), high tree species diversity, and mature stand structure.

Biologically, it is clear that mature heterogeneous forest communities with high tree species diversity were decidedly important for sun bears and indicated a strong affinity for interior forests. Areas with significantly more bear activity had at least a 4-fold higher diversity of trees selected by bears ("bear trees") and the least dominance by particular tree species and families. Regardless of elevation, bear activity was significantly higher in areas with higher overall tree diversity, moderate tree stand densities, and greater tree maturity, girth (dbh), height, and canopy cover. There was also a higher abundance and basal area of emergent and crown trees in sites with significantly more bear activity. Cover, forage availability, and mature stand structure were the most important biogeographic effects at all elevations. But, the most significant influence was the interactive effect of habitat disturbance on these parameters, which accounted for the majority of variance in bear activity in optimum bear habitat < 500 m asl, whereas most bear activity was > 500 m asl.

7.4 Competitive and Agonistic Influences

Interactions and use of habitat by potential sympatric competitors and antagonistic species can influence bear movements, behaviour, health, survival and fitness. As with other Ursidae, the dominant form of competition for sun bears is probably for space and food, especially in the form of fruit and termites for sun bears. Yet, tests revealed that, regardless of habitat, competitor presence, diversity and abundance were insignificant influences on sun bear habitat use. Essentially, there was almost 90% overlap among bears and their most significant sympatric competitors.

In addition to niche expansion to take advantage of arboreal fruit sources, the evolution of sun bear arboreal behaviour and general landscape use has also been potentially influenced by the co-evolutionary forces of predation and agonistic interactions. The odds of sun bear activity occurring in areas with predator activity were higher than if predators were not present, but predator and antagonistic species overlap with bears was less than 10%. Such minimal overlap indicates that, ecologically, the chance of predators occurring in the same areas with bears may simply be coincidence due to environmental characteristics or cues, such as food, which attracts bears as well as prey that attract predators.

Despite coincidence, bear activity was potentially influenced by the presence of tigers and leopards, but any possible exclusionary effects were not geographic. Sign and camera-trapping data showed that bears occurred within one metre of tigers and leopards and this activity may be temporally influenced. Minimum camera-capture periods between bears and tigers were ≥ 3 days apart and about 6 hours apart between bears and clouded leopards.

Sample size may have affected these results. Despite thousands of hours of cameratrapping, capture rates were low for bears as well as tigers and leopards. Sign-surveys also revealed that the total frequency of tiger and leopard signs were only about 9% relative to total bear signs. Two possibilities require consideration:

- (1) Statistically, the disparity in sign sample sizes (91%) between bears and felids may have biased these results.
- (2) Ecologically, these data may indicate: (A) population densities are low leading to minimal overlap and (B) the probability of overlap between these wide-ranging species at fine spatial and temporal scales may be naturally low (i.e. about 10%). Thus, chance encounters may be even less because tiger and leopard ranges can be > 3 4 times larger than sun bear ranges in these ecosystems.

7.5 Habitat Disturbance

The direct and interactive effects of habitat disturbance on sun bear ecology and landscape use were consistently the most significant influences in tests across all variables, regardless of habitat type, ecosystem, biogeographic condition, site, area, or region. The type, intensity, age, and geographic extent of disturbances accounted for at least 85% of the variation in sun bear signs when examined separately from other independent variables, such that the most dominant effects in these models were the distance and timing of the disturbance relative to where and when bears were active. When habitat disturbance was tested in models with other biogeographic parameters and human activity, habitat disturbance consistently remained the most dominant interactive effect, accounting for the significant majority of the variance in bear signs in all cases. In these multivariate models, the distance and timing of disturbance relative to where and when bears were active remained the most significant interactive influence.

In undisturbed sites, tree species diversity, forage abundance, mature stand traits, and cover were the most important biogeographic effects on sun bear habitat use. It is generally known that bears will risk areas with less cover and security for a reward such as alternative food sources (Craighead *et al.* 1995, Servheen *et al.* 1999). Reports of bears entering local gardens suggest that such risks remain true for some sun bears (Fredriksson 2005), but this activity was insignificant in this study. Some bears used post-disturbed areas, but this was predominantly in older regenerated forests in advanced successional stages, and use of these areas was still significantly less compared to undisturbed primary forests. Bear use of secondary forests only approached relatively low or moderate levels when those secondary forests were > 25 years old and were contiguous with undisturbed primary forests.

In general, I found that observations of sun bears using post-disturbed forests should be considered relative to the forest's age and frequency of use by the bears. Results demonstrated that habitat use by sun bears in post-logged areas was directly correlated with the age of the disturbance. When more succession occurred in regenerating forests there was correspondingly more bear activity, beginning with minimal or limited activities by relatively few bears about 15+ years after less intensive disturbances, such as low-impact selective logging. This habitat use pattern was also observed for other major competitors and antagonisitic species, including bearded pigs (*Sus barbatus*), binturongs (*Arctictis binturong*), pangolins (*Manis javanica*), civets (Viverridae spp.), Sambar (*Cervus unicolor*), muntjacs (*Muntiacus* spp.), mouse deer (*Tragulus* spp.), porcupines (*Hystrix brachyuran*), gibbons (*Hylobates* spp.), orangutans (*Pongo pygmaeus*), tigers (*Panthera tigris sumatrae*), marbled cats (*Felis marmorata*), bay cats (*Felis badia*), and clouded leopards (*Neofelis nebulosa*). While a few of these species and others were present in more mature secondary forests > 20 years old, they were statistically more abundant in undisturbed primary forests. Species important to local communities for protein, such as bearded pigs, were observed at low frequencies in forests selectively logged 5–10 years earlier, but pig abundance increased substantially with forest age or less/no disturbance. Tiger and clouded leopard activity in areas with most forms of human disturbance was minimal to non-existent. There were no photo captures of either species in such areas and, in the few cases with signs, these were observed immediately adjacent to primary forests at very low frequencies (< 0.01% of signs).

In undisturbed sites, sun bears primarily occurred where there was cover and rich and diverse food sources, but in sites affected by disturbance bears occured in more secure areas rather than productive areas. This pattern was consistent across all study sites and provides insight into nutritional stress and mortality issues blamed on naturally stochastic influences, such as the 1997 – 1998 El Niño Southern Oscillation (ENSO) event and asynchronous or aseasonal fruit productivity (*see* Wong 2002, Fredriksson 2005). In areas where there is disturbance, habitat loss or fragmentation, there is a possible synergistic interaction between disturbance and naturally-low food productivity affecting bears.

7.5a Forage and Forest Clearing

Forage diversity and availability are highly important for Ursidae, including for sun bears. Wong (2002) suggested that the poor physical condition and mortality of some sun bears observed in his study resulted from a prolonged scarcity of fruit in Danum Valley (438 km²), Sabah. Fredriksson (2001, 2005) suggested similar nutritional deficiencies in the Sungai Wain Protection Forest (100 km²) in East Kalimantan. In these cases, it was proposed by Wong (2002) and Fredriksson (2005) that a prolonged period of extreme fruit lows followed masting episodes and the El Niño Southern Oscillation event in 1997 – 1998. As a result, the reproductive ecology of key inter-mast fruit species (particularly figs) was disrupted for up to two years (Harrison 2001) and may have affected bears and other wildlife (Meijaard *et al.* 2005). However, in areas with abundant food availability, such as in large contiguous primary forests > 8,000 km² like Kayan Mentarang and Gunung Leuser National Parks, bears were in good physical condition during the height of the 1997 – 1998 El Niño and through to 2004 (Augeri 2003, LMU unpubl. data, S. Wulffraat pers. comm.).

Camera-trapping (2001 - 2004) and hunting records (1997 - 2003) in all survey sites of this study indicated very fit sun bears in all age classes, with high fat content, burnished coats, and adults with multiple off-spring. Other species, such as bearded pigs, were also in much better condition in Kayan Mentarang and Gunung Leuser National Parks than those observed in smaller areas like Danum Valley. All species photographed in these larger protected areas during 2001 - 2004 appeared fit and in healthy physiological condition.

Figures 7.1 – 7.3 illustrate the extreme physical differences between photographed bears and pigs in these large protected areas (> 800,000 ha) (figure 7.1) compared to those photographed by Wong (2002) in the small 43,800 ha Danum Valley, which is surrounded by over 1 million ha of selectively-logging and cleared forest. Wong's study occurred during 1999 – 2001 (which overlapped with the current study data of 1997 – 2004), and photographs there show extremely emaciated and malnourished bears and pigs (figures 7.2 and 7.3). Wong (2002) reported that at least 50% of bears captured were in poor or very poor condition, with significant weight loss of at least 32%. Captured and observed bears had sparse hairs and protruding ribs, vertebrae, zygomatic arches, hipbones, and scapulae. According to Wong (2002), such poor conditions were clear signs of malnutrition and at least 33% of Wong's captured bears died during this period.

During this period, bears in the 1,400,000 ha protected area of Kayan Mentarang National Park, which is part of the southern portion of the ecosystem comprising Danum Valley (Meijaard *et al.* 2005), were in very good physical condition (figure 7.1), despite effects from the same Bornean-wide drought, fires, presumed fruit shortages, and the 1997 – 1998 El Niño Southern Oscillation event (Augeri 2003, S. Wulffraat pers. comm.). Bears in the 800,000 ha Gunung Leuser National Park in northern Sumatra also appeared to be in very good physical condition during this same period (figure 7.1), despite similar regional effects from the El Niño event, fires, and drought (Augeri 2002, LMU unpubl. data).

Fredriksson and Wich (in review, as cited in Meijaard *et al.* 2005) suggest that availability of mast fruiting species is a key factor in sustaining sun bear health, particularly during inter-mast periods, but results from the current study showed that disturbance could have a more proximate effect on sun bear forage availability, abundance, and diversity than natural stochastic events, such as low fruiting years. Forest clearing can play an important and sometimes dominant role in the ecological dynamics of interior forest and edge communities. Disturbance has been observed to induce micro-climatic changes that can affect seed production and dispersal, flowering, and fruit abundance and diversity, especially in small or isolated forests (Lovejoy *et al.* 1986, Augeri 1995, Laurance and Bierregaard 1997a, Bierregaard *et al.* 2001, Laurance *et al.* 2001, 2002).

Data from this study as well as from the WWF – Indonesia Kayan Mentarang Project (S. Wulffraat pers. comm.) and the Leuser Management Unit (unpubl. data) indicate that, during this period (1997 – 2003), animals in large contiguous forests and reserves were in good condition with normal to high sub-coetaneous and bone marrow fat content, no mange or disease, lustrous coats, and offspring. In disturbed areas adjacent to the reserves and in smaller forest patches, however, landscape-level disturbance effects may have influenced key forage productivity and its availability for bears and other species.







Figure 7.1. Sun bears photographed by remote camera-trapping in this study. Top: Gunung Leuser National Park December 2001; middle: Gunung Leuser National Park, May 2002; bottom Kayan Mentarang National Park, June 2003.



Figure 7.2. Sun bears photographed by remote camera-trapping (top and middle photos) and during telemetry recapture (bottom photo) by Wong (2002) in Danum Valley, Sabah during 1999 - 2001 (© 2002 Wong).





Figure 7.3. Bearded pigs photographed by remote camera-trapping. Top: this study in Kayan Mentarang National Park June 2003. Bottom photo by Wong (2002) in Danum Valley, Sabah during 1999 – 2001 (© 2002 Wong).

Chapter 7

Discussion

For example, all forests around Danum Valley and Sungai Wain have been heavily logged, cleared or converted to agriculture, roads, and development and a significant proportion of fruit-bearing species have been removed. In Sungai Wain, fires and encroachment reduced the effective available habitat within the reserve by 60%, leaving only about 40 km² of primary forest, obliging bears to search for alternative foods (Fredriksson 2005). Sun bears and pigs in small forest patches and logged forests in Vietnam have also been observed to be significantly malnourished (L. Thang Ha pers. comm.). When such small forests are adjacent to, or are surrounded by, extensive logging and forest clearing, edge effects and other disturbance dynamics can influence forage availability (Lovejoy *et al.* 1986, Augeri 1995, Laurance and Bierregaard 1997, Gilbert and Setz 2001, Santamaria Gomez 2004). Such factors force species like sun bears with a predominantly frugivorous diet to be more dependent on other food sources, including those outside of the reserve.

Stochastic episodes leading to local food shortages for bears can be exacerbated by forest loss and other disturbances (Mattson *et al.* 1996, Craighead *et al.* 1995, Craighead WWI 2000), including for sun bears (Meijaard *et al.* 2005). This is especially true in small forest patches and reserves. In contrast, fruit productivity data from this study showed that large tracts of contiguous undisturbed forests (e.g. Kayan Mentarang National Park, Gunung Leuser National Park) had higher availability and diversity of fruit-bearing trees across a larger and more accessible landscape, probably because these areas are able to maintain less disturbed and more stable micro-climatic conditions with a higher probability of available foods dispersed over wider areas (Lovejoy *et al.* 1986, Bierregaard *et al.* 2001, Laurance *et al.* 2002, Meijaard *et al.* 2005). Thus, stochastic events, such as the absence of mast-fruiting over a long period may not create as significant an effect in larger areas as in smaller forest reserves subject to disturbance (Bierregaard *et al.* 2001, Meijaard *et al.* 2005).

Results from this study showed that some older secondary forests were relatively productive, more so than other areas, but in general this productivity was homogeneous and dominated by relatively few forage groups and species. Fruits were significantly more diverse and bee hives and visible termite colonies were more abundant in primary forests. When all principal sun bear foods were examined together, overall forage was more diverse and proportionally more available in large tracts of primary forests. Such diversity is critical in the Tropics, where food availability is both spatially and temporally patchy.

In the Tropics, seasonality and patchiness affect the availability of major bear foods, where fruits are subject to asynchronous and aseasonal phenology and the abundance of secondary items at the micro-site level compensates for the loss of more preferred items. Forest clearing can affect the ecological dynamics of interior forest communities (Lovejoy *et al.* 1986, Hamilton 1999, Laurance *et al.* 2001, 2002, Bierregaard *et al.* 2001) enough to

disrupt the abundance, diversity and availability of these foods. Such effects can influence protected areas, such as Sungai Wain and Danum Valley, which are small "habitat islands" with high edge:area ratios relative to the surrounding influential landscape of cleared forest, agricultural areas, logging, and development (Laurance *et al.* 2001, 2002).

For example, the small 43,800 ha Danum Valley conservation area is surrounded by over 1 million ha of selectively-logged forest (Wong *et al.* 2004) and thousands of hectares of cleared and planted oil palm plantations (Augeri pers. obs.). Parts of Danum Valley have also been selectively-logged. These effects on such large scales can induce microclimatic changes over extensive areas that alter, for example, fruit availability in adjacent "undisturbed" primary forests (Augeri 1995, Laurance and Bierregaard 1997, Laurance 2001, Rankin-De Mérona and Hutchings 2001, Meijaard *et al.* 2005). At < 5,000 ha of effective available habitat for bears in Sungai Wain (Fredriksson 2005), the isolation and edge influences there may be more substantial. Sun bears primarily occur where there is a rich and diverse food source, but in situations such as those observed in small forest areas adjacent to or surrounded by disturbance and forest clearing, such disturbances can affect fruiting patterns, productivity, and distribution as well as access to these and other resources.

For the majority of bear species, food availability and diversity, habitat condition, and cover are frequently the most prominent ecological factors influencing habitat use. Environmentally-stochastic events, such as primary food resource failures, can influence bear health, movements, mating, recruitment, and population dynamics (Jonkel and Cowan 1970, Rogers 1976, 1987, Craighead *et al.* 1995, Powell *et al.* 1997), some of which have been observed in Borneo (Wong 2002). Fruit availability is clearly an important food item for sun bears and alternating drought and rain influence fruit productivity in the Tropics, particularly dioecious (pioneer) and other figs, which are an important resource for sun bears and other species throughout the forest and year (Fredriksson 2001, Augeri 2002, Wong 2002). The effects of such stochastic events, including El Niño, may be exacerbated by logging, forest loss, fire, and other disturbances. For sun bears, forest clearing can:

- (1) Prevent access to more seasonally productive areas or those relatively unaffected by drought or other stochastic events.
- (2) Reduce the diversity, abundance, and availability of key foods, such as fruit, bee hives, and termites in logged areas, border habitats, and in the core zones of small forest patches or reserves.
- (3) Exacerbate the effects of drought and other stochastic events, both locally and regionally, by inducing further micro-climatic changes.

- (4) Create drought-like effects and conditions, or influence other local microclimate conditions, such as changes in temperature, humidity, wind, and light incidence. These conditions can impact floral biology, and subsequently, flower and fruit productivities in interior and edge forests.
- (5) Provide access for hunters and village expansion.

These and other effects can influence the nutritional stability of bears and where they move and forage across the landscape (Jonkel and Cowan 1970, Rogers 1987, Craighead *et al.* 1995, Powell *et al.* 1997, Wasser *et al.* 2004). This is especially true for bears restricted to small forest reserves or patches (Merrill *et al.* 1999, Craighead *et al.* 2001, Larkin *et al.* 2004, Meijaard *et al.* 2005). During stochastic events, such as occasional low fruit productivity in South-East Asian forests, there is probably a synergistic interaction between these episodes and habitat disturbance from large scale forest clearing. Significantly malnourished bears and other wildlife have been observed in small forest patches and disturbed areas across South-East Asia (pers. obs., L. Thang Ha pers. comm.). These sites are relatively small (< 200 km²) and it is possible that this synergistic interaction between low fruit productivity (perhaps induced by ENSO or other stochastic events) and extensive logging and forest clearing in the surrounding landscapes has affected some populations.

7.5b Edge Effects

Several studies report that the biophysical effects of logging (e.g. microclimate changes and increased temperature, wind turbulence and sun light) can affect flora and fauna hundreds of metres inside a forest from its edge, lasting for generations (Lovejoy et al. 1986, Chen et al. 1992, Wiens 1992, Augeri 1995, Laurance and Bierregaard 1997, Laurance 1999, Rankin-De Mérona and Hutchings 2001, Laurance et al. 2001, 2002, Bierregaard et al. 2001). For example, the highest proportion of tree mortalities within 300 m of edges in Amazonian tropical forests was of large mature trees that comprised only 1.8% of all trees, but as much as 23.4% of all estimated above-ground biomass (Laurance et al. 2000). There was a 281% faster rate of mortality in these large trees when they were within 300 m of forest edges than in interior communities (Laurance et al. 2000) and, in some cases, large tree deaths occurred more than 500 m from the edge (W.F. Laurance pers. comm. 2002). According to several studies (see Hamilton 1999, Laurance et al. 2000, 2001, 2002, Bierregaard et al. 2001, Sist et al. 2002), increased tree mortalities in fragmented tropical forests can reduce fecundity and gene flow of canopy and emergent species, induce proliferation of pioneer and exotic species, reduce forest volume and structural complexity, and alter biogeochemical cycling and greenhouse-gas emissions.

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In general, forest clearing, canopy openings, and abrupt edges can create the effect that even forests several thousand hectares in size are virtually all edge by substantially reducing the area:edge ratio (Wiens 1989, 1992, Chen *et al.* 1992, Augeri 1995, Harrison and Bruna 1999). Consequently, biological processes as well as individuals and species within patch interiors are affected (Lovejoy *et al.* 1986, Gosz 1991, Wiens 1992, Forman and Moore 1992, Laidlaw 2000, Crooks 2002). Whether in the Amazon or South-East Asia, the long-term effects of edge creation, canopy openings, soil compaction and loss, biomass reduction, tree mortalities, and respiration and transpiration changes from forest loss can be significant on biotic communities (Wilson and Wilson 1975, Rijksen 1978, Davies and Payne 1982, Wilson and Johns 1982, Terborgh 1983, Johns 1983, Lovejoy *et al.* 1986, Johns and Skorupa 1987, Gilbert 1994, Laidlaw 2000, Gilbert & Setz 2001, Laurance *et al.* 2001, 2002, Bierregaard *et al.* 2001, van Schaik *et al.* 2001, Robertson and van Schaik 2001, Meijaard *et al.* 2005).

Edge effects clearly influenced sun bears. Analyses demonstrated a strong linear relationship in which sun bear habitat use rose significantly as distance from the edge of disturbance increased and it did not reach consistently high levels until > 10 km from intense disturbance. In all sites and ecosystems on Sumatra and Borneo, mature undisturbed interior forest characteristics were dominant factors in micro-site and habitat type use by sun bears. These stand traits, especially a predominance of cover, mature fruiting trees and tree species diversity, were characteristic of undisturbed primary forests and were key components in the bear's habitat use, as well as potentially important indicators of interior forest affinity for bears. As such, they may be prominent influences on sun bear home range needs.

Fruiting within and between tree species in the Malay archepelego occur at different times and localities (MacKinnon *et al.* 1996, Whitten *et al.* 2000). Thus, sun bear home range core locations and exploratory activity on the periphery of their ranges may be correlated with seasonal and annual shifts in food availability and abundance, particularly relative to edges. Adjusting their home ranges to include a high diversity of potentially fruiting trees may ensure a fitness advantage for some bears. Although some bear home ranges may appear "fixed", especially during relatively short-term observations of months or even a few years, they often shift to accommodate seasonal and annual forage needs across an individual's life time (Rogers 1976, 1987, Powell 1987, Powell *et al.* 1997, Craighead *et al.* 1995, Mattson *et al.* 1996, Mace *et al.* 1999). While this observation requires further study in relation to sun bears, this ranging strategy could be a potential reason for the very high diversity of forage, especially fruiting trees, observed in areas where sun bears were most active, thereby enabling a higher probability of fruit and alternative forage availability within the bear's range across seasons and years.

These results were consistent with Servheen (1989) and Fredriksson (2001), who noted that densities and diversities of primary sun bear foods, including termites, ants, beetles, and fruit decrease with increased fire, logging, and other disturbances. In addition, I found that edge effects can directly and indirectly affect the geographical ecology of sun bears through availability of, and access to, these primary resources.

In the Danum Valley, Sabah Hussin (1994) observed that figs, an important sun bear fruit resource, were notably more abundant in primary forests (3 trees/ha) than in post-selectively-logged areas (1.75 trees/ha) 10 years after logging ended. Hussin also found that species richness and fruit production in general were significantly higher in primary forests than in the surrounding post-logged areas. A subsequent study in the same area by Ahmad (2001) on forest composition and structure showed that species richness was slightly higher in areas 10 years after logging ended. The latter richness, however, was dominated by younger pioneer species, many of which do not provide substantial food sources for sun bears at such young stages of development. My results revealed that such younger forests types are low in bear forage and are also marginal for security, canopy and escape covers, while also being highly dense in under-story vegetation that limits movement for larger species.

Results from this study concur with Fredriksson (2001) and Wong (2002) that alternative foods other than fruit, such as termite colonies, beetles, bee hives and ants, are important foraging resources for sun bears throughout the year and especially during intermast periods. However, we observed these to be less abundant in young, newly-logged areas and edges. Fredriksson (pers. obs. as cited in Meijaard *et al.* 2005) reported that there were lower densities of above-ground termite colonies and stingless bees in recently logged areas in East Kalimantan. Subterranean termite colonies are a major food source for bears, where < 20% of observed termites consumed by sun bears in the Sungai Wain Protection Forest, East Kalimantan were from visible termite mounds (Fredriksson *in litt*, as cited in Meijaard *et al.* 2005). But, logging and associated effects (e.g. soil compaction, desiccation, etc.) appear to cause a decline in the abundance of these colonies, especially at higher levels of disturbance (Jones *et al.* 2003) and closer to edges.

7.5c <u>Fire</u>

Fires are a severe form of habitat disturbance affecting the region. Several studies show that the direct damage from forest fires in logged areas is more severe than in unlogged areas. Further, a forest's susceptibility to fires increases with logging activities due to changes in micro-climate, increased fuel loads, and increased human access (Leighton and Wirawan 1986, Woods 1989, Cochrane 2001, Siegert *et al.* 2001, Ross *et al.* 2002). Cochrane (2001) suggests an obvious synergism between forest fragmentation and fire poses significant threats to tropical ecosystems.

Smoke, ash, flames, and heat from extensive forest fires on Borneo have increased over the past two decades from logging operations, local agriculture, development, and large-scale commercial plantations. The smoke from these fires on Borneo is extensive, blanketing much of South-East Asia on an annual basis. On its own, smoke can influence light penetration, respiration, transpiration, moisture retention, seed production, flowering, fruiting, and micro-climates (Kay et al. 1994). Furthermore, susceptible species could be replaced by exotic fire-resistant and pioneer species that provide fewer resources to native wildlife, including bears. The most dominant effect is that, as forests become more fragmented, remaining forests are far more susceptible to edge effects, which negatively influence remaining forest dynamics as much as 2.5 km in interior forests and increase vulnerability to more fires (Cochrane 2001). Some authors suggest that large-scale tropical forest fires could be considered equal to a large-scale edge effect (Laurance 2000, Cochrane 2001). In just four months in 1997 – 1998, about 52,000 km² of land area burned in East Kalimantan alone, 26,000 km² of which were forests (Fredriksson 2005). Thus, it is likely that fires have influenced flowering and fruiting on a notable extent across Borneo and reduced available effective unburned habitat for sun bears in many areas, including in primary forests adjacent to plantations, logging concessions, and high human-use zones.

7.6 Time Mosaic

Depending on the degree of disturbance, edge effects were strongly correlated with disturbance timing. The intensity and timing of disturbance were significant variables associated with sun bear habitat use throughout all study sites and habitats. Essentially, bear activity was at insignificant levels or was non-existent at closer distances to disturbed areas < 15 years old. The more time selectively-logged forests had to regenerate and produce cover and key food resources, the less influential distance became and the more bears used these areas. Compared to remote interior forests, bear activity reached only low to moderate levels once (a) less disturbed forests were > 20 - 25 years old and were structurally similar to more mature forests and/or (b) when primary forests were > 5 km from younger disturbed areas.

The oldest secondary forests observed in this study were about 40 years old, but bear activity was still insignificant in these areas. Results showed clearly that low to moderate levels of bear activity in post-disturbed areas required > 25 - 30 years following the disturbance.

There was no bear activity in heavily disturbed areas, such as young clear-cuts < 15 years old, and only minor bear activity in low to moderately disturbed primary forests areas (i.e. reduced-impact logging) beginning an additional 10 years after such minor disturbances. Bear activity was higher in stands that had some regeneration and primary productivity and were allowed to re-establish for more than 20 - 25 years. Although Wong *et al.* (2004) concluded that sun bears occur in logged forests in Danum Valley, the degree of "occurence" relative to the overall population was not established. Further, their observations were **(1)** for only one area and **(2)** were in forests that were *selectively* logged 10 - 20 years earlier and were adjacent to or mixed within undisturbed primary forests. Consequently, cover, security, and food were available to varying degrees. I found that in every area we surveyed in East Kalimantan and northern Sumatra, cleared forests required longer periods to regenerate and produce primary forage and it took longer periods for bears to begin using those forests with a statistically significant degree of consistency. Thus, across the landscape, effective available sun bear habitat appears to be arranged in a time-space mosaic of suitability.

7.7 <u>Relative Habitat Use</u>

It is important to consider the frequencies of individual bears among different habitat types relative to forest age and the overall population. Some observations have been reported of sun bear occurrence in secondary forests or disturbed areas (Wong 2002, Wong *et al.* 2003, Fredriksson 2005), but the ages of these forests, as well as the scale and frequency of use by these bears relative to their overall populations, are important factors when analysing population-level patterns. Results from the present study showed that the significant majority of sun bear activity in post-disturbed areas was predominantly in older heterogeneous forests that retained some primary forest traits and had substantial time to regenerate and evolve through older succession stages that provide mature forest structure.

The overwhelming majority of bear signs, photographs, and all genetic samples were observed in undisturbed primary forest regardless of habitat, ecosystem, site, or region. When examined across all sites, < 10% of signs were observed in secondary forests and only 0.73% were in areas < 15 years old. The significant majority of signs in secondary forests were in forests > 20 - 25 years old and more than 74% of these were > 1,000 m from any form of disturbance. Less than 2% of all signs were within 50 m of forest edge bordering disturbed areas < 1 year old and there were no observations of any kind in highly disturbed areas. Demographic data also revealed that primary forests had more diverse and abundant

bear size/age classes with consistently larger bears. In contrast, bear size/age classes in forests affected by disturbance were more homogeneously composed of smaller bears and the signs were more clustered and of similar apparent origin, suggesting relatively few bears with concentrated activity.

Results concur with those of several other studies (Wilson and Wilson, 1975, Wilson and Johns 1982, Johns 1983, Normua *et al.* 2003, 2004) that indicated sun bears predominantly occur in primary forest. Wong *et al.* (2004) extrapolated across the sun bear's global range, concluding that the importance of primary forests for sun bear survival is uncertain and that bears clearly occur in logged forests. In contrast, telemetry study at another site in Sabah around logged forests and an oil palm estate showed that the preponderance of sun bear activity (88%) was spent in interior primary forests (Normua *et al.* 2003). Observations by Wong (2002) and Wong *et al.* (2004) were limited to a sample of four male bears, which were localised in the same general area in one site, and the majority of information was gathered primarily from just two bears. Observations of the other two bears were only for 2 - 4 months and occurred within one dry season (Wong 2002). Only telemetry data from one bear were adequate enough to examine monthly activity patterns, which was for about 6 months (Wong *et al.* 2004). Thus, data on bear activity beyond this one area and season were limited. Such extrapolation across a species' entire global range and population from only two bears from one site should be considered with caution.

Because trapping success and subsequent capture probabilities are accepted as primary indicators of, and are used for, abundance estimates, Wong's low sample size could indicate a very low frequency of bears using that area of post-selectively logged forest. In fact, Wong *et al.* (2004) concluded "trapping success was low (1 bear/396 trap nights), probably due to the low density of sun bears in the study area and their wariness." This observation also could be due to many of the same factors associated with results in the current study. It is important to emphasise that the forests in Danum Valley had 10 - 20 years to regenerate after selective logging, but the bears were in extremely poor health. Ultimately, observations of sun bears using post-disturbed areas should be considered relative to the age, type, and extent of the disturbance, along with the condition, age/sex, and number of bears relative to the overall population in the area. The preponderance of data in the current study from > 50 habitat types and conditions in selectively-logged forests, secondary forests (of all ages), agricultural areas, clear-cuts, edge habitats, swamps, and primary forests in 16 different sites on both Borneo and Sumatra demonstrated that the overwhelming majority of bear activity was in undisturbed primary forests.

Some sun bear activity cannot be observed, especially in areas where bear signs are cryptic or unobservable by humans due to certain habitat characteristics. Normua *et al.*

(2003, 2004) reported that sun bears observed by radio telemetry in an oil palm estate in Sabah fed only on fallen fruits at night, leaving few signs behind and then returned to the adjacent forest before light. Bears reported to feed in local gardens often follow a similar activity pattern. Thus, sign-surveys alone may not accurately identify habitat use in such areas and may be biased to where people are active. Such bias was minimised in this study by the large number of independent random samples in multiple habitats and sites in a randomised experimental design using site-occupancy modelling and method plurality *via* a combination of camera-trapping, sign surveys, and genetic sampling over multiple years.

It is important to note that all agricultural and disturbed areas reported used by sun bears in this study and others (Normua *et al.* 2003, 2004, Fredriksson 2005, LMU unpubl. data) were adjacent to relatively intact primary forests where bears were most active. Normua *et al.* (2003) reported that bears in his study "spend most of their time in the deep forest", where 74% of all radio locations and at least 88% of 24 hour telemetry monitoring were located. Minimum home range estimates from Normua's telemetry observations showed that these bears spent the majority of their time in interior forests > 1-2 km from the edge. Because his telemetry observations were limited to the forest edge road and all attempted locations within the oil palm estate were presumed successful, it is likely that these bears probably spent more time interior. Thus, when the bears were absent from the estate and border areas of 1 - 2 km from the edge, Normua *et al.* (2003) concluded that they were further inside the forest beyond telemetry range. In fact, 72% of attempted locations

Essentially, the number of sun bears and the frequency of their time spent using disturbed areas are minimal. Normua's telemetry observations were also based on only four bears, one of which was lost after 2 months of monitoring. As in Wong's (2002) study, the low sample size in the Normua *et al.* (2003, 2004) study must be considered with caution, but capture rates by Normua around the estate may indicate a correspondingly low frequency of bears in those disturbed areas relative to the overall bear population.

A key aspect of the current study was aging the signs, particularly relative to disturbance or other variables like the presence of people, predators or competitors. In other studies, workers have observed bear signs in secondary and edge forests and inferred that bears were present in high numbers (G. Fredriksson pers. comm., S.T. Wong pers. comm.). One bear can generate much sign, however, and if these are not properly aged it is unknown (1) how many (or few) bears generated those observed signs and (2) if those signs indicated bear activity before, during or after the disturbance. In many disturbed areas in the current study, older signs remained for as along as 10 years or more and showed that bears had been active in those areas prior to disturbance. Yet, no signs were observed in those same areas

once they were highly disturbed less than one year before. Less than 1% of observed bear activity occurred in areas that had regenerated for less than 15 years.

Despite extensive geographic coverage over thousands of hours and 4 years of camera-trapping, there were no photographs of sun bears or other large carnivores in disturbed areas or secondary forests of any age in these study sites. About 93% of all signs in the current study were in undisturbed primary forests and, in the few disturbed areas where signs were observed, almost 94% of these were generated by bears *prior* to when the disturbance occurred. Thus, aging signs relative to when disturbance occured is important for determining tolerance and actual use of such sites. Further, the vast majority of these latter signs (86%) that were in areas potentially affected by disturbance were still > 500 m from the disturbance. Of all 4,886 signs recorded across all study sites, habitats, and ecosystems, only 0.32% (n=16) were observed within 10 m of a disturbed area < 1 year old. Given the highly consistent and corroborative results across all parameters and tests, it is clear that any habitat use of disturbed areas and secondary forests in this study was minimal and by relatively few bears. Habitat disturbance was the most significant and dominant effect on sun bear habitat use, movement patterns, distribution, and abundance in these areas.

7.8 Virtual Fragmentation

Although it is tempting to relate the theoretical and behavioural aspects of predatoravoidance behaviour by sun bears to their avoidance of humans, results showed that sun bears occurred within one metre of their most significant natural predators, where such overlap may have been temporally spaced. In contrast, there were significant geographic effects on bear avoidance of people and results support the Risk-Disturbance hypothesis (Gill *et al.* 1996, 2001, Gill and Sutherland 2000, Frid and Dill 2002) outlined in Chapter 3.

Results showed that increased human access by trails and logging roads with corresponding increases in human activity influened bear habitat use, both geographically and temporally. In addition to increasing mortality of bears and other species by increasing access for hunters, increased levels of consistent human activity (> 25 - 50 people present/week) in high-quality habitats appears to have negatively affected sun bear use of those same areas, effectively fragmenting the bear's range without any habitat disturbance. Depending on the site, moderate to high levels of human activity without any habitat disturbance appeared to create a form of *Virtual Fragmentation* for sun bears.

A strong linear relationship existed in which bear habitat use was lower with correspondingly higher levels of human activity. There was significantly more habitat use by sun bears with farther distances from human activity and the bears appeared to be avoiding highly productive habitats, including in primary forests without habitat disturbance, that had

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persistently moderate to high levels of human use. It may be assumed that hunting has affected bears in these areas, but in several highly productive sites where bear hunting did not occur and where there were other human activities, bear use of these areas was insignificant, if at all. This relationship also occurred in remote areas where bears were normally more active, but where there was moderate trail use by people (10 - 25 people present/week) and/or gathering of non-timber forest products. In such areas, there was no hunting, but bear activity was significantly reduced. Bears in these remote areas may not be habitutated to human presence and may avoid sites more consistently associated with people.

When comparing similar habitats with and without human presence, the same pattern held across all sites. One of the best examples is trail use. It has been proposed by other observers that trails in rainforests are preferred by most large mammals, including by bears and felids (Y.M., Robertson pers. comm.). Results from this study do not support this assumption for sun bears in these sites. Proportionally, there were significantly more signs and photographs off trails than on. Even comparing game trails and human trails in the same habitats and sites, there was a two-fold higher use by bears of game trails ($\overline{x} = 42.9$ sign/ha) than human trails ($\overline{x} = 21.9$ sign/ha). In the east plain ecosystem of Gunung Leuser National Park, where some of the most highly productive sites in this study were located, there was high human use (> 50 people present/week) with correspondingly lower sign frequencies $(\overline{x} = 3.75 \text{ sign/ha})$ and no camera-trapping photographs. This same pattern was found in the East Kalimantan study sites. In Kayan Mentarang National Park where habitat disturbance is minimal to non-existent, high quality primary forest areas with moderate to high human use had the least amount of sun bear signs, even though these areas retained the same habitat characteristics of sites with high bear use in remote locations without human use. In some cases, forage diversity and abundance was highest in these areas least used by bears and the only significant effect was found to be persistent human presence. In remote sites without human presence, there was a 2 - 4 fold higher mean sign frequency/ha. In all areas where habitat disturbance did not exist, highly productive mature forests with correspondingly moderate to high human use ($\geq 25 - 50^+$ people present/week) had little to no bear activity.

Many sensitive species in Indonesia adjust their ranges temporally to human activities, including sun bears, tigers, and other interior or forest-dependent species (Griffiths and van Schaik 1993, Normua *et al.* 2003, 2004). In addition to temporal adjustments and given occupancy model assumptions, both sign and camera-trapping results from this study revealed that, in the majority of sites, sun bears were minimizing their use of, or avoiding areas with, moderate to high levels of human activity. This behaviour has also been observed in other bear species (Augeri 1994, Mattson *et al.* 1987, 1996, McLellen and Shackleton 1988, Servheen *et al.* 1999, Craighead *et al.* 2001). Such avoided areas retained most or all

of the habitat character associated with more frequent sun bear use of undisturbed forests, such as high degrees of cover, more abundant and diverse forage, and mature heterogeneous tree stand character. Habitat bias was minimal because factors such as tree species, topography, stand character, and so forth were similar. Yet, both sign and camera-trapping results showed that habitat use in these sites was minimal to non-existent. In fact, bear activity in the same habitats increased significantly, even with moderate distance (100 - 500 m) from these areas, but did not reach normal levels until > 1 km away.

More research is needed regarding this observation, but if this pattern holds it may indicate that a more cryptic effect of anthropogenic disturbance is influencing sun bear movement patterns in areas without habitat disturbance. For many species, including migratory organisms or highly-vagile species like sun bears with coevolved adaptations to specific habitat types, such habitat avoidance can simulate actual habitat fragmentation.

7.9 Habitat Compression

In the majority of these study sites, a pattern of "compression" or "funnelling" effects were observed in some narrow or restricted undisturbed areas with physical barriers (e.g. rivers, steep rocky valleys, narrow watersheds). Analyses revealed higher concentrations of bear signs derived by bears in the same size/age class in these areas, where camera-trapping also resulted in higher frequencies of photo captures of the same bears. In contrast, similar habitats in larger unrestricted areas had lower concentrations and more dispersed signs, and camera-trapping and demographic analyses indicated these signs were by different bears or were associated with different size/age classes. These results suggest that, in undisturbed settings, effects associated with compression by natural barriers may concentrate bear activity.

In restricted areas, a form of *Habitat Compression* may be inducing densitydependent spatial patterning among individuals and subsequently aggregating bear activity. Distribution tests demonstrated that sun bear signs in continuous primary forests without significant physical barriers were randomly dispersed within sites, but signs were significantly aggregated within the majority of secondary forests, edge habitats and other areas affected by disturbance. In those disturbed areas where bear signs did occur, sign frequencies/transect were significantly lower while sign densities/ha were higher and more concentrated. Test results of Distance-sampling data revealed that encounter rates in undisturbed areas were significantly lower, possibly indicating dispersed activity, whereas disturbed sites were significantly higher by more than 58%, indicating potential clustering.

Figure 7.4 illustrates an example of sign clustering along a transect in a small primary forest area of ca. 100 ha in the Bulungan Research Forest, East Kalimantan, which

was subject to Reduced Impact Logging (RIL) practices several years earlier. This transect was typical of survey results in areas affected by disturbance. Chi-square tests confirmed that sun bear signs in these disturbed primary forests and other disturbed areas, secondary forests, edge habitats, and so forth, were significantly clustered along transects (P < 0.02). As shown, relatively few signs occurred in these sites and, where they did occur, bear activity was clustered further away from the disturbance. Productivity surveys in these sites revealed that **a**) forage was widely dispsered and **b**) forage abundance was often similar or perhaps higher in the disturbed areas, but bears tended to avoid such sites.



Figure 7.4. Schematic representation of actual survey, S013, in primary forests disturbed by Reduced-impact logging (RIL) practices several years earlier in the Bulungan Research Forest, East Kalimantan. Blue dots were all observed sun bear signs on the transect and orange-hatching was RIL-logged area. This type of clustering was typical in such sites. Chi-square tests confirmed sun bear signs in these and other disturbed primary forests, secondary forests, edge habitats, and so forth, were significantly clustered along transects (P < 0.02).

It is important to stress that a high concentration of observed bear signs does not necessarily correlate with a high number of bears, as reported by some workers (Fredriksson pers. comm., Wong pers. comm.), and may only indicate concentrated activity by particular individuals within their range. Sign frequency *versus* sign density can be quite different. For example, there were significantly lower sign frequencies in areas affected by disturbance, but when considered by unit area there was a two-fold higher concentration of signs in these sites than in primary forests. In secondary forests and small primary forest patches adjacent to disturbance, and so forth, there was a mean of 58.92 signs/ha *versus* 29.23 signs/ha in large undisturbed primary forests where signs were more dispersed.

The high sign density in smaller patches and areas affected by disturbance does not indicate a higher abundance of bears or preferred use. On the contrary; the majority of signs in this study were randomly distributed in primary forests, which also had more diverse and abundant size/age classes. Habitat and population compression is probably causing bears in these disturbed areas and small forest patches to aggregate their activities in smaller available habitat.

Telemetric studies on sun bears have not gathered sufficient information regarding possible range-partitioning in which some bears focus on core areas or forces other bears into less preferred sites. The latter commonly occurs among bears where more dominant individuals control and defend the highest-quality habitats, forcing out intruders (which are most often subdominant smaller, younger, less healthy, or weaker individuals) and obliging the latter individuals to inhabit less productive areas. For some examples of this dynamic see: (a) *Ursus americanus*: Jonkel and Cowan 1970, Rogers 1976, 1987, Kasworm and Manley 1990, Augeri 1994, Powell 1987, Powell *et al.* 1997; and (b) *Ursus arctos*: Jonkel 1984, Augeri 1994, Craighead *et al.* 1995, Mace and Waller 1997. Results from this study of size/age class demographics indicated larger sun bears were more abundant in primary undisturbed forests compared to smaller patches and areas affected by disturbance.

The high sign densities in areas affected by disturbance were not due to more aggregated forage in the latter areas. It would be expected that, regardless of habitat type or disturbance, areas with clustered forage would have aggregated bear sign distributions corresponding to forage concentrations. In fact, > 86% of transects had significantly dispersed or no cover of key bear foods, such as fruit, termites, and bee hives. Further, bear signs were randomly distributed in large primary undisturbed forests whereas signs were consistently and significantly clustered in smaller patches and areas affected by disturbance, despite dispersed or minimal coverage of principal food items. Such high sign densities were also not due to higher mean forage productivities in secondary forests, edges and so forth because, despite the importance of food, the significant majority of sun bears were clearly avoiding these areas. Essentially, in the few instances where bears occurred in such areas, the high sign density/unit area could be the result of *Compression Effects*.

Figure 7.5 illustrates this relationship. In Indonesia, a variety of anthropogenic (logging, village expansion, agriculture, roads) and natural (fire) factors reduce effective available sun bear habitat, while also isolating remaining patches (figure 7.5A). Any remaining bears are subsequently "funnelled" or "compressed" into smaller patches and their activities become more concentrated in tighter ranges (figure 7.5B). With fewer resources in smaller areas, isolated patch populations decline over time, but the foraging and movements of remaining bears are compressed. Although there are fewer bears, their ranges may be smaller and overlapping. Thus, their density/unit area may appear higher and more concentrated than in large contiguous forests. Remaining patches become insular and forage usually declines, as seen in Sungai Wain (Fredriksson 2005) and Danum Valley (Wong

2002), and both population and physiological stresses can increase. This relationship causes (1) some bears to foray outside of the patch and (2) the relatively spurious assumption that signs were created by a large number of bears. In contrast, larger areas will be less susceptible to outside disturbance and will enable more bears to be more widely dispersed.





Figure 7.5. (A) Illustrates various anthropogenic and natural means by which habitat is lost and compressed. (B) Shows that remaining patches exposed to the same disturbances are compressed along a pressure gradient, exerting stronger effects on smaller patches, which concentrates the activities of fewer bears into smaller areas. This can increase densities/unit area, causing some bears to foray outside of the patch. By contrast, larger areas are less susceptible to the same external disturbances and enable more bears to be more widely dispersed. Different coloured dots represent the signs of different bears. Different sized arrows and border lines indicate greater or lesser influence. Lighter green areas and orange borders indicate degraded areas and edge effects, respectively.

This phenomenon may explain the tight home range patterns of sun bears in small forest reserves, such as those reported for the 100 km² Sungai Wain Protection Forest, East Kalimantan (Meijaard *et al.* 2005), where the bears have also been observed in edge areas and local gardens (Fredriksson 2005). In the current study, sun bears are avoiding use of or movement through such disturbed areas, but in smaller patches, forage and habitat losses could force bears into marginal edge habitats and human-cultivated areas for food. Use of such areas can lead to nutritionally-stressed sun bears or human-caused bear mortalities. Although use of marginal habitats was either non-existent or statistically minimal in this study, the relatively few sun bears occurring in these areas were associated with the smallest size classes and their activities appeared localized and aggregated in tight, potentially compressed, ranges. By ranging within these disturbed and human inhabited areas, these bears and their offspring may also be growing habituated to human presence. Thus, they may be risking both physiological stability (by using marginal areas) and potentially high costs of conflicts with people.

Results support the Perturbation-Stress hypothesis outlined in Chapter 3. Changing contiguous primary forests into a discontinuous patch-work of disturbed and undisturbed areas bordered by abrupt, sharply contrasting edges can induce geographic and density-dependent compression. This can alter a bear's movement dynamics through the landscape and prohibit critical habitat use (McLellan and Shacklton 1988, Augeri 1994, 2000, Mattson *et al.* 1996, Merrill *et al.* 1999, Boyce 2000, Augeri 2002b). Ultimately, compression can create insular effects, possibly increase stress levels in individual bears, and exert notable pressure on the population. Reduced food density, availability or access can influence bear health, movements, mating, recruitment, and population dynamics (Jonkel and Cowan 1970, Rogers 1976, 1987, Craighead *et al.* 1995, Powell *et al.* 1997, Wasser *et al.* 2004) and can increase physiological stresses on the bears (Cattet *et al.* 2003, van der Ohe *et al.* 2004, Owen *et al.* 2004, Wasser *et al.* 2004). Increased stress levels in remaining bears can be exacerbated by the population-level and demographic consequences of habitat fragmentation. Thus, patch insularity and associated human disturbance can lead to a more rapid decline in longevity, fitness, and persistence.

7.10 Habitat Uniformity and Population Distribution

Whether in theory or practice, two common assumptions are (1) organisms are evenly distributed across the landscape and (2) the landscape is relatively homogenous. Depending on the species, these assumptions can sometimes be used for general density and abundance estimates, particularly on a theoretical level, but neither of these assumptions is ecologically realistic. In reality, most organisms, mammals in particular, have naturally irregular distributions due to differences in forage distribution and habitat or effects from population pressures (e.g. density dependence), competition, predation, or climate (MacArthur 1972, Thrall *et al.* 2001). Results are consistent with this supposition and demonstrated that the distribution of sun bear habitat use between undisturbed forest areas is patchy. This begs an important question for conservation biology: If an organism has a naturally patchy distribution, why would habitat fragmentation be a problem?

Many species, particularly mammals, focus their activity in certain locations or core areas due to very specific micro-habitat characteristics that provide suitable or preferred foods, denning and nesting sites, mates, and interspecific dynamics. Radio telemetry, signs, and field observations indicate many species, including large carnivores (e.g. Ursidae, Felidae, Canidae, among others), move throughout their home ranges and territories, but all show that a high proportion of their activities are focused in specific core areas, at least on a seasonal or annual basis. Note that this is different than forced aggregated or compressed activity described above. For felids and canids it is more often a flexible central portion of a defended territory, whereas for other species, such as bears with semi-overlapping ranges, it can consist of less-well defined "centres" or "patches" that may shift seasonally or annually.

First, many biologists and conservationists present specific densities and distributions using estimates based on 'blanket' or generalised coverage of an entire area without having surveyed or quantified the actual proportion of occupancy. These general estimates can be inaccurate, particularly for genera like bears that have semi-defined or overlapping ranges and disparate distributions based on forage distribution, security, den sites, potential mates, and so on. In some cases, there may be abundant concentrated food(s) where individuals of the same population may overlap and share those resources. It is well-documented that, even for aggressive genera like bears, high food abundance or diversity increases tolerance of conspecifics. Essentially, whether there is high overlap among individuals or absolute competitive exclusion in defined territories, the most common reality is variable and patchy population distribution across the landscape.

Second, most habitats are diversely structured and this heterogeneity leads to increasing variance in population distribution at broader landscape scales (figure 7.6). For example, as habitat features increase in variance, specific sites will become more or less

attractive than others, concentrating and dispersing individuals across the landscape. Some areas will be more occupied with possible overlap or aggregation among individuals, whereas others sites will be relatively unused or will function as transit corridors. There can often be portions of the landscape that are relatively unsuitable and are essentially unused by that species. Consequently, home ranges or territories will not be uniformly distributed across the landscape.



Figure 7.6. Hypothesised relationship between population distribution and landscape heterogeneity. Ecological realities suggest that most species will have a patchy distribution across the landscape based on habitat variances, where forage diversity and abundance, competitive and demographic pressures, habitat differences, etc. will influence an individual's movements and focal activities, site selection, and subsequent distribution patterns.

Third, bears have patchy distributions, often with concentrated seasonal or annual activity in specific locations, which can change over an individual's life-time (Jonkel and Cowan 1970, Bunnell and Tait 1981, Rogers 1977, 1987, Mattson *et al.* 1987, McLellan and Shacklton 1988, Beak 1989, Craighead *et al.* 1995, Mattson *et al.* 1996, Noss *et al.* 1996, Craighead and Vyse 1996, Powell *et al.* 1997, Craighead WWI 2000, Craighead *et al.* 2001, Merrill *et al.* 1999, Waits *et al.* 1999, Boyce *et al.* 2001, Augeri 1994, 2003, Meijaard *et al.* 2005). For sun bears in undisturbed areas, patchy distributions are associated with microhabitat traits, such as tree stand structure, diversity, and maturity level, dead biomass, or elevation gradients. Such habitat features will concentrate termite colonies, ant colonies, and bee hives, optimise fruit productivity, or will provide suitable ground cover, canopy cover, security, and topography.

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Although occupied bear habitat in contiguous undisturbed forest is relatively "patchy", this secure continuous forest facilitates the bears' capacity and behavioral choices to move between good micro-habitat sites and access valuable resources across a continuous forested landscape over seasons and years. This ability to move between high-quality microhabitats, in turn, provides a higher probability for reproductive success and fitness. In contrast, forest fragmentation from development, roads, clear-cuts, fencing, and plantations blocks access to necessary resources and reduces bear movements through the landscape (Noss et al. 1996, Anderson 1997, Beausoleil 1999, Merrill et al. 1999, Bader 2000, Murrow 2001, Augeri 1994, 2003, Larkin et al. 2004, Meijaard et al. 2005). These situations can also create population "sinks", such as (a) local gardens, garbage areas, etc. that may attract bears and provide other resources where human-bear interactions result in bear mortality or (b) an area with diminished resources where a bear may be "forced" or compressed into the area due to disturbance, social, or forage needs, but access to other areas may be blocked, resulting in health decline or mortality. Both of these scenarios and others have been observed in numerous areas with bears and other large carnivores (Mattson et al. 1996, Noss et al. 1996, Powell et al. 1997, Craighead et al. 2001, Merrill et al. 1999, Servheen et al. 1999, Bader 2000, Boyce et al. 2001, Augeri 1994, 2003, Meijaard et al. 2005).

Thus, the difference between a naturally patchy distribution and one that is caused by fragmentation is that in a contiguous undisturbed landscape, bears can still move between suitable habitat to access resources and mates despite a lack of preferred resources between good sites. In a fragmented landscape the capacity for bears to access resources and suitable habitat may be limited or blocked beyond the borders of a truly isolated "island" patch surrounded by disturbance, inhospitable terrain, or intensive human activity (Craighead et al. 2001). If an isolated patch is small, it could lead to compression or insular effects. Deteriorated bear health and survival can result along with increased mortality, diminished reproductive capacity, inbreeding depression, and conflicts with humans, among other deleterious effects. Such fragmentation problems lead to reduced recruitment into that site's bear population and, in the long-term, possible extinction of that sub-population (Craighead and Vyse 1996, Craighead et al. 1998, Waits et al. 1999, Servheen et al. 1999). In either case, the loss of bears can cause wider population impacts on a regional level (Boyce et al. 2001). This can also result in ecological impacts on the community, such as reduced seed dispersal and nutrient cycling, along with altered competitive and predatory dynamics (Augeri 1994, Terborgh et al. 1999, 2001).
7.11 Sun Bear Distribution, Density and Abundance

It can be concluded from these analyses that sun bear use of disturbed and nonforested areas, young secondary forests, edges, agricultural areas, clear-cuts, and so forth was insignificant relative to the overall population and landscape use. At a landscape scale habitat loss will obviously produce clumped distribution of bears between suitable and unsuitable areas (figure 7.7). At the micro-habitat level sun bear activity was randomly dispersed within primary forests, but was clustered in disturbed sites. Yet the majority of primary forest sites (87.5%) at the landscape level also had significantly patchy sign distribution among occupied areas. Essentially, sun bear distributions in these sites are patchy and fragmented across the landscape matrix.



Figure 7.7. Aerial view of typical patchy landscape in East Kalimantan, Borneo.

The density and distribution analyses in this study were based on (1) a large number of independent random samples in multiple habitats, ecosystems, regions, and years, (2) empirically-tested theory and models of detection probabilities and the proportion of area occupied in particular study sites, which accounted for patchiness and gaps between individuals, and (3) method plurality, redundancy, and testing with other data. It must be emphasized that the models used to produce these density and abundance estimates are based on several assumptions and rely on telemetry-based home range data from a small sample of bears (n=4) from another study and site on Borneo (*see* Chapters 5 and 6). Although the models and methods used in this study were tested and shown to be robust and ecologically realistic, the estimates should only be generalised across these particular study sites. Given this and other caveats noted previously (*see* Chapters 4 - 6), some inferences can be made about sun bear distributions in these sites based on the preponderance of data and analyses:

- (1) Consistently occupied sun bear habitat is mainly in undisturbed primary forest, whereas bears most often avoid highly disturbed areas.
- (2) Sun bears are randomly distributed within primary forest, but populations are patchy at landscape levels. Where bears occur in secondary forests and sites affected by disturbance and high human use, bear activity is generally clustered or "compressed".
- (3) The majority of occupied areas are in more remote and less accessible primary undisturbed forests at elevations between 400 1,000 m asl, most likely due to high intensity disturbance and human use < 500 m asl.
- (4) Due to loss of suitable habitat, sun bear ranges are highly fragmented across the overall landscape. Such ranges are mostly limited to specific areas within undisturbed primary forest and shift on a seasonal and annual basis. Where some bears are using older secondary forest (>20 30+ years old) this is minimal relative to the overall population and its landscape use.

According to these models, the most densely populated area in this study was Kayan Mentarang National Park (0.0416 bears/km⁻²), followed by the Bulungan Ecosystem (0.0246 bears/km⁻²) and then Gunung Leuser National Park (0.0234 bears/km⁻²). Given model assumptions and limitations and assuming 50% range overlap among adults, abundance estimates for Kayan Mentarang National Park are about $873 \pm SE$ 197.1 adult bears. In Bulungan there may only be about $156 \pm SE$ 48.6 adult bears, and in Gunung Leuser National Park there are an estimated $280 \pm SE$ 61.2 adult bears.

To my knowledge these are the first empirically-based density and abundance estimates of sun bears and this is the first study of bears using occupancy modelling, such as that proposed here and by MacKenzie *et al.* (2002), to produce these estimates. More than 50 habitat types and conditions were surveyed in 16 study sites across six regional ecosystems on Borneo and Sumatra. These estimates are based on the estimated proportion of consistently occupied habitat in these study sites, account for gaps between ranges, and are consistent with published densities for the sun bear's closest phylogenetic relatives *Ursus americanus* and *U. thibetanus*, as well as for *U. arctos, Melursus ursinus*, and *Tremarctos ornatus* (Powell *et al.* 1997, Servheen *et al.* 1999, Kattan *et al.* 2004). Although tests revealed the data and models in these analyses are robust and ecologically realistic, density and population figures reported here should be viewed cautiously as estimates with associated error and assumptions previously noted (*see* Chapters 4 - 6).

7.11a Updating Sun Bear Status for IUCN Red List

The preponderance of results from this research indicate fragmented and low sun bear populations in this study region, which are largely restricted to older or undisturbed habitats. *Helarctos malayanus* has been listed as Data Deficient by the IUCN Bear Specialist Group since 1996 according to IUCN Red List Categories and Criteria version 2.3 (1994), but this research in its entirety provides sufficient information to update *H. malayanus* listing. Based on Gärdenfors *et al.* (2001) and the Guidelines to Application of IUCN Red List Criteria at Regional Levels (2001), Bornean and Sumatran island bear populations are isolated from conspecific populations outside of the region. The extinction risk for these populations is considered identical to that of an endemic taxon and the most recent IUCN Red List Categories and Criteria version 3.1 (IUCN 2001) can be used without modification for a regional assessment. But, if relisting is considered, Red List geographic range criteria (VU B1 and VU B2) are not applicable for this regional situation. Only Vulnerable category C is applicable. Thus, if these methods, related assumptions, and the full range of population estimates and associated standard errors for these sites are considered for a new assessment, *H. malayanus* could be possibly categorised in Indonesia as Vulnerable (VU), based on:

• C2ai: the estimated population is < 10,000 mature individuals (C), with a projected or inferred decline (2) and no sub-population mean is > 1,000 mature individuals (ai).

Considering such low abundance estimates in the largest protected areas remaining in the sun bear's global range, smaller sub-populations may be considered Endangered (EN, based on criteria B1bi-v, C2ai and D) or Critically Endangered (CR, based on criteria B1a and B1bi-v) in areas where they are fully isolated. Because populations in other countries are highly fragmented (Servheen 1999a), it is possible that bears in these regions are Endangered (EN) or Critically Endangered (CR) according to similar criteria. These data also support the CITES Appendix 1 listing that *H. malayanus* is in danger of extinction and is or may be affected by international trade. Given the bear's strong affinity for primary forest and the increasing rate of forest loss throughout its global range, prudence and legal guidelines dictate scientifically-based conservation measures should be implemented without delay.

It should be noted that the reality of population estimates is that they are approximations and the reality of animal distributions is that they are patchy. Very few species or taxa, if any, occupy 100% of their range and have perfectly uniform distributions. Most individuals in a population have different ranges that vary across seasons, years, and habitats, often with gaps between individual ranges. Forage abundance and availability, security, mate distribution, topography, and the distribution and availability of suitable habitat, among other factors, all determine where species will occur in particular densities.

The current estimates are empirically-supported, are based on the predicted proportion of occupied area, and apply only to these study areas. Nevertheless, these estimates cannot account for the precise degree of patchiness or overlap among individual bears and, thus, assume some degree of inference. Some assumptions exist in the models along with the applicability and error of home range estimates of a small sample of bears from another study and site on Borneo (*see* Chapters 4 - 6). While tests in the current study show the data and models in these analyses are robust, it is stressed that density and population figures reported here are not absolute numbers and should be viewed cautiously as estimates with associated error and assumptions. These estimates provide only a baseline, for which further research should examine and validate by comprehensive multi-year mark-recapture studies in representative habitat types and conditions throughout the bear's range.

7.12 Habitat Loss and Fragmentation

Habitat loss, disturbance, and fragmentation are considered the most pressing issues in conservation biology (Meffe and Caroll 1994, Noss et al. 1996, Laurance and Bierregaard 1997a, Whitmore 1997, Wiens 1997, Hanski and Gilpin 1997, Laurance 1999, Cuaron 2000, Bierregaard et al. 2001, Soulé and Orians 2001), including in Sumatra (Whitten et al. 2000, Robertson and van Schaik 2001), Peninsular Malaysia (Laidlaw 2000), and Borneo (MacKinnon et al. 1996, Meijaard et al. 2005). About 50% of Indonesia's forests are fragmented by development, extractive industries, agriculture, roads, and other human constructs (WRI 2004). Whitmore (1997) noted that by 1996, the greatest deforestation impacts within Asia were on the forests of the Malay Archipelago, which included Indonesia with a loss of 18,000 km²/year. At least 85% of these areas were primary forests logged for the first time. Whitmore estimated that, between 1981 and 1990, the Malay Archipelago lost a total of 204,000 km² of tropical forests, including 173,000 km² of lowland rain forests, 11,000 km² of seasonally-moist lowland forest, and 19,000 km² of hill and montane forest all of which are principal habitats for sun bears and many other threatened species. In 2004, the World Resources Institute (WRI) estimated that since 1996 the rate of forest loss in Indonesia had increased from 18,000 km²/year to about 20,000 km²/year (WRI 2004).

According to WRI (2004), Indonesia is experiencing one of the highest rates of tropical forest loss in the world. The archipelago was still densely forested as recently as 1950, but 40% of the forests existing in 1950 were cleared by 2000, decreasing from 1.62 to 0.98 million km^2 of forest cover. All analyses suggest that forest loss is accelerating. A mean of about 10,000 km^2 /year were cleared in the 1980s, but by the early 1990s this increased to about 17,000 – 18,000 km^2 /year. In January 2003, the Jakarta Post reported that

deforestation in Indonesia was about 24,000 km² in 2002, up from an average of 20,000 km² in previous years (Jakarta Post 14/1/03).

Indonesia's lowland forests are the most at risk. These regions are the richest in timber resources and biodiversity and WRI (2004) estimated that, if current trends continue, the remaining unprotected lowland forests in Kalimantan will disappear by 2010. Protected areas are also under increasing threat (Robertson and van Schaik 2001). Robertson and van Schaik (2001) and van Schaik *et al.* (2001) predict that at the 2000/2001 rate of forest loss in the Leuser Ecosystem, the world's largest orang-utan population could be extinct by 2011.

No accurate estimates are available for forest cleared by small-scale farmers, but a WRI estimate suggested that shifting cultivators might have been responsible for about 20% of forest loss, or about 4 million ha between 1985 and 1997 (WRI 2004). It is important to note that forest clearing by small-scale farmers is a notable source of deforestation, but the annual average has been ca. 307,692 ha, which accounts for only about 1/5 of the total deforestation in Indonesia (WRI 2004). The majority of loss is due to timber extraction, large-scale commercial agriculture, town and village expansion, and other extractive industries. By 2004 more than 16% (160,000 km²) of Indonesia's remaining natural forests were approved for conversion to industrial timber plantations or agricultural plantations (WRI 2004). In many cases, forest conversion contradicted laws that required plantations to be established on only degraded land or on forest land already allocated for conversion.

The gap between legal supplies of wood and global demand is filled by illegal logging. Expansion of Indonesia's pulp, plywood and paper industries has created a demand for wood fibre that exceeds legal supplies by 35 - 40 million m³/year (WRI 2004). Such expansion, as well as government decentralization, has facilitated illegal logging (McCarthy 2000, van Schaik *et al.* 2001, Robertson and van Schaik 2001), which has consumed at least 10 million ha of forests (WRI 2004). Many wood processing industries openly acknowledge their dependence on illegally-cut wood (Robertson and van Schaik 2001), which accounted for about 65% of the total supply in 2000 (WRI 2004). According to McCarthy (2000), a 1999 joint Indonesia-UK Tropical Forest Management Programme report estimated that illegal timber extraction totalled 30 million m³/year, or half of all timber extraction in Indonesia. This estimate is only what could be counted; the true amount is probably substantially more because illegal logging is pervasive and the timber is difficult to track.

According to recent statistics from the Indonesian Ministry of Forestry, legal timber supplies from natural production forests declined from 17 million m³ in 1995 to under 8 million m³ in 2000 (WRI 2004). This decline was offset by timber from forests cleared for industrial plantations. The Global Forest Watch (2004) notes that industrial timber plantations are widely promoted and subsidised to supply the world's demand for pulp

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products. In practice, more than 200,000 km² of forest have been cleared since 1985. Almost 90,000 km² of land, most of which is primary forest, has been allocated for development as industrial monoculture timber plantations, and about 20,000 km² have been planted with a handful of fast-growing species like *Acacia mangium* to produce pulpwood. WRI (2004) reports that an additional 7 million ha of forest were approved for conversion to estate crop plantations by the end of 1997. At least 2.6 million ha were converted to oil palm plantations since 1985 and new plantations of other estate crops add 1 - 1.5 million ha.

Transmigration programmes have cleared substantial amounts of forest to relocate people from over-crowded Java to the outer islands to create large-scale commercial agriculture plantations and other projects. These projects cleared > 20,000 km² of forest for resettlement between the 1960s and 1999 (WRI 2004). Once relocated immigrants serve their contracted time working for the transmigration programme, they can be allocated their own 5 ha plots to farm (Augeri 1991). It is more common, however, for many of these immigrants to use the transmigration programmes as a free way to move out of the cities and then quit the project to farm and hunt illegally, clearing more and more forest every few years once the tropical soils become too nutrient-poor to cultivate (Augeri 1991). Illegal migration and settlement by pioneer farmers at the margins of logging concessions, along roads, and in national parks has increased since 1997 (Robertson and van Schaik 2001, WRI 2004), but reliable national-scale estimates of forest clearance by pioneers are not available. Many of these farmers are unfamiliar with the more sustainable rotation farming techniques of local indigenous peoples, such as the many Dayak cultural groups on Borneo, and the results are eroded and denuded soils that may never support and restore native forests.

Large-scale plantation owners also use fire as a cheap and easy method of clearing forest for further planting. Deliberate fire-setting, combined with abnormally dry conditions by El Niño events, led to uncontrolled wildfires of unprecedented extent and intensity in the 1990s. More than 50,000 km² of forest burned in 1994 (WRI 2004) and an estimated 52,000 km² of land burned in East Kalimantan in just four months during 1997 – 1998, of which 26,000 km² were forests (Seigert *et al.* 2001, Fredriksson 2005). In March 2003, local papers reported more than 900 fires were burning across Kalimantan (pers. obs.) and, according to satellite images (WRI 2004) and ground surveys (D.M. Augeri unpubl. data), some of this land is regenerating only as scrubby forest and much hasn't been recolonized.

Although Indonesia and Malaysia preside over most of the remaining sun bear habitat, these vast and diverse countries contain two of the highest and most dense human populations in the world and are commercial distribution sources for tropical hardwoods (Santiapillai and Santiapillai 1996, WRI 2004). This study confirms that sun bears occur in most undisturbed lowland forest types in Indonesia and, by 1997, Meijaard (1997) suggested

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there had been a 30 - 60% loss of suitable sun bear habitat on Borneo since 1960. In Sumatra, Whitten *et al.* (2000) estimated that by 1984 up to 80% of the lowland forests had been lost, and Santiapillai and Santiapillai (1996) noted that by 1988 the remaining lowland forest on Sumatra had been decreased to only 10% of the total land area of the island. Between 1985 – 2000, the Leuser Ecosystem lost ca. 565,000 ha of primary forest and, at this rate, about 77% of the ecosystem's primary forest would be lost by 2030 (LMU unpubl. data). According to Meijaard (1997), most of Borneo's forests were earmarked for logging and conversion to plantations or agricultural land by 1997, except for 7.0% of Kalimantan (MacKinnon *et al.* 1996), 1.9% of Sabah, and 0.8% of Sarawak (Collins *et al.* 1991), all of which are theoretically protected. Disturbance to, and the loss of, individuals and habitat are exacting more immediate effects on sun bears in other countries (Servheen *et al.* 1999).

The net result of this forest loss and degradation is increasingly-fragmented habitats (MacKinnon *et al.* 1996, Santiapillai and Santiapillai 1996, Whitten *et al.* 2000, Laidlaw 2000, Augeri 2003, WRI 2004, Meijaard *et al.* 2005) with escalating effects of insularity (Harris 1984). For the majority of bears island biogeographic effects can be significant. Habitat loss blocks or reduces their ranging ability between preferred areas and increases pressures on the population, particularly if bears are isloated in small patches and marginal areas or during environmental constraints from forage crop failures, drought or fire – all of which can naturally reduce major bear food sources and suitable habitat (Jonkel and Cowan 1970, Rogers 1987, Augeri 1994, Craighead *et al.* 1995, Powell *et al.* 1997). Because bear fecundity, reproductive rates, and recruitment rates are among the lowest of terrestrial mammals (Nowak 1991), such insular pressures can impact fluctuating populations (Rogers 1976, 1987, Allendorf *et al.* 1991, Craighead *et al.* 1995, Craighead and Vyse 1996).

Restricted movements among fragmented patches can limit the sun bear's capacity to forage, maintain nutritional stability, mate, and facilitate cub recruitment into the population. When such pressures occur during a natural population ebb, or in periods when hunting, fires, drought, limited mast fruiting, or habitat loss decrease a population or reduce demographic ratios for viable reproductive mates within or among fragmented areas, long-term sub-population and metapopulation persistence could decline (Rogers 1987, Craighead and Vsye 1996, Powell *et al.* 1997, Mattson 1998, Boyce 2000, Murrow 2001, Maher *et al.* 2003, Larkin *at al.* 2004). Regardless of deleterious genetic consequences, the demographic effects from these events could lead to local bear sub-population extinctions (Servheen *et al.* 2001, Murrow 2001, Larkin *et al.* 2004) and threaten sun bear persistence and evolutionary potential. All other bear species have been negatively affected by habitat loss, fragmentation, and human activities (Servheen *et al.* 1999) and by 1999, the IUCN Bear Specialist Group

concluded that the sun bear may become extinct in many parts of its range before its existence is even documented (Servheen 1999a).

7.13 <u>Reserve Network</u>

These results clearly demonstrate that temporal and geographic buffers are needed for sun bears in these areas. Depending on disturbance intensity, habitat type and geography, a minimum of 30 years are required for forests to sufficiently regenerate to support bears at low to moderate levels, and primary interior forests need to be > 5 km from intensive disturbances of > 5 ha. The following guidelines for a time-space mosaic can help planners with a set of ecologically sound reserve networks for the reality of such managed landscapes.

Density and abundance estimates in this study indicate that current protected areas of $14,000 \text{ km}^2$ may only be supporting means of about 800 - 1,000 bears in East Kalimantan and 500 - 600 bears in North Sumatra and Aceh. Data from some areas suggest that small populations may exist in sites of at least 100 km^2 (Fredriksson 2001), but the size and longevity of such populations are uncertain due to increasing insularity. Regardless, IUCN guidelines state that reserves need to be $> 100 \text{ km}^2$ to minimise extinction risk.

Numerous undisturbed sites should be represented across the landscape and include all habitat types in the region. Reserves need to be greater than 200 km² with low edge:area ratios and should be connected to or contiguous with much larger protected areas > 10,000 km² (figure 7.8). The latter areas are critical for insuring general population stability and source areas for sub-population exchange to maintain demographic and genetic diversities.

Buffers zones free of habitat disturbance need to be more than 5 km wide and should be included in all management and conservation plans. Beginning at the protected area boundary, buffers should start as primary forest and can transition to older secondary forests > 25 - 30 years old that are allowed to fully regenerate, and finally to less suitable habitats on the edge of disturbed areas (figure 7.8). Edges can be environmentally-sound agroforestry projects, such as produce that are unpalatable to most wildlife, but should comprise < 5% of the area. This can include products like organic shade-grown tea or coffee in ecologically-beneficial tree plantations composed of indigenous plants and trees that provide habitat for non-depredating wildlife and support surrounding forest dynamics. Importantly, these areas should not provide suitable forage for bears and should be unattractive. Garbage and other foods should be disposed in bear-proof containers that can be easily transported and dumped in proper sites elsewhere. Such agro-forestry will be a natural protective barrier for wildlife while excursions outside of the protected area will be less desirable for bears, thereby reducing human-bear conflicts. These areas will also provide income for local communities, which can help reduce illegal incursions into the protected area. This realistic zoning will reduce deleterious edge effects on primary forests while maintaining forest stability, but it is emphasised that sun bears spend the significant majority of their observed time (88%) (Normua *et al.* 2003) and habitat use (92.7%) in undisturbed interior forests. Thus, the amount of undisturbed natural forest cover in the landscape should be proportionally larger than all other uses in the area. It is also stressed that tree plantations and agro-forestry projects are not a substitute for natural forests, should be < 5% of the area, and should not be included in proportional estimates for natural-forest cover.



Figure 7.8. Practical application of reserve network in Indonesia. Primary forest with black boundaries represent protected areas, which should support all habitat types in the region and have buffer zones at least 5 km wide composed of primary or secondary forests > 30 yrs old. Large protected areas > 10,000 km² serve as critical source populations (large bear symbols) for smaller outlaying reserves (small bear symbols), which should be greater than 200 km². Agro-forestry of non-palatable products to wildlife is a natural barrier and provides income for local communities.

Depending on the distance between reserves, corridors should be greater than 8 - 10 km wide, which is large enough to reduce some edge effects on either side and support transient individuals during temporary migrations. These reserves, buffer zones, and corridor areas will also protect local communities against stochastic environmental episodes and natural disasters and will provide more healthy forest and ecosystem services, particularly clean water and non-timber forest products. A series of these networks will protect sun bears and a diverse array of wildlife across the landscape. The latter include locally important migratory species (e.g. bearded pigs) and other endangered forest-dependent species, such as tigers, leopards and other felids, most primates, elephants, and rhinoceros, to mention a few.

CHAPTER 8

IMPLICATIONS And CONCLUSIONS



"Scientists recognize that habitat loss and its inevitably associated fragmentation collectively pose the single greatest threat to earth's biological diversity." Bierregaard et al. (2001a) "The fault, dear Brutus, is not in our stars, but in ourselves, that we are underlings." Shakespeare, Julius Caesar (I, ii, 140-141)

8.1 Implications

Like most species, if left undisturbed with sufficient resources and habitat, sun bears would thrive. Yet, bears in these areas appear to be choosing security over food. This research shows that habitat fragmentation, edge effects, and loss of suitable habitat and food resources can directly and indirectly affect sun bear movement patterns and ecology. Consequently, sun bear persistence and evolutionary potential could be affected in these areas.

The conversion of forests by timber harvesting, agriculture, road networks or development can subdivide animal populations and subject them to deleterious environmental, demographic, and genetic effects (Saunders *et al.* 1991, Augeri 1994, 1995, Hanski and Gilpin 1997). This is especially important for bears that depend on viable habitat corridors and minimal inter-patch distances to enable sub-populations to interact as a single large population (Boyce 2000, Murrow 2001, Craighead *et al.* 2001, Mahre *et al.* 2003, Larkin *et al.* 2004). Limited exchange among geographically-isolated sub-populations can subsequently result in local extinctions of bears within isolated patches (Murrow 2001, Larkin *et al.* 2004) and/or extinctions of those populations (Craighead and Vyse 1996, Waits *et al.* 1999, Boyce 2000, Craighead *et al.* 2001).

Conventional and selective-logging practices in the Malay Archipelago destroy a high proportion of both target and surrounding trees (Whitten *et al.* 2000, Sist *et al.* 2002) and such damage can affect important sun bear foods, such as fruit, termite and ant colonies, bee hives, beetles, and grubs. In Malaysia, Johns (1983) found that, with just 3.3% selective tree removal, 50.9% of the forest was "destroyed" and there was a severe perturbation causing the loss of large numbers of species from the community. Whitten *et al.* (2000) reported data from Sumatra showing that, to achieve an 8% log harvest, 54% of the forest was completely destroyed or badly damaged. In the Bulungan Research Forest, a controlled comparison of Reduced-Impact Logging (RIL) and Conventional Logging (CNV) practices revealed that an average of 37.9 and 50.8% of the original tree populations in the respective treatments were either damaged or killed, and skidding accounted for a significant proportion of new canopy openings and damage to non-target trees (Sist *et al.* 2002). The forest floor is also affected by logging, skidding, and road building, all of which lead to substantial soil loss and compaction, as well as removal of necessary biomass, nutrients, and detritus (Whitten *et al.* 2000, Laurance 2001, Sist *et al.* 2002). Combined, these disturbances can

affect remaining floral communities (Bierregaard *et al* 2001, Laurance *et al*. 2001, 2002) and result in the reduction or elimination of important sun bear food resources and habitat. Human activities, noise, and other disturbances associated with logging up to one kilometre away negatively influence sun bear use of highly productive habitats in those areas.

When combined with stochastic events, such as periodic droughts or fires, these types of disturbances can affect population and evolutionary viabilities (Gilpin and Soulé 1986, Allendorf *et al.* 1991, Frankel and Soulé 1992, Craighead and Vyse 1996, Holt 1997, Hedrick and Gilpin 1997, Paetkau *et al.* 1998, Merrill *et al.* 1999). Given that sun bear populations are significantly reduced and may be isolated in fragmented patches over their range (Servheen 1999a, Chapters 6 and 7), the fate of local bear populations depends on our ability to predict how landscape structure and disturbances affect bear movement patterns within and among patches (Wiens 1992, 1996, 1997, Augeri 1994, Noss *et al.*1996, Craighead and Vyse 1996, Stacey *et al.* 1997, Boyce 2000, Bader 2000) and their access to critical resources and habitat (Rogers 1987, Craighead *et al.* 1995, Powell *et al.* 1997, Boyce and McDonald 1999, Mace *et al.* 1999).

If compression effects exist in some areas with disturbance, or if virtual fragmentation is occurring from moderate to high levels of human activity in areas without any physical habitat disturbance, several implications associated with habitat fragmentation and island biogeograhic effects may induce negative metapopulation dynamics. In particular, endothermic species such as sun bears must be active and have access to habitat(s) across a landscape on a constant basis to search for resources. Habitat selection, which is based on resource and foraging choices, cover and security, mating, and so forth is manifest in space and time over an animal's home range, ultimately affecting reproductive success and fitness. Accordingly, the size of, distribution, and access to high-quality habitats help an individual contribute disproportionate numbers of offspring and genes to future generations, i.e. fitness.

Primary sun bear food sources, such as fruit and termites, are only available in certain areas and/or at certain times of the year. Consequently, bears require unrestricted access to forage across the landscape on a constant basis to enhance their persistence. If suitable bear habitat and resources are decreasing or are blocked due to habitat loss, fragmentation and disturbances, or if bears are forced to risk security by using secondary, edge, marginal, human inhabited, or disturbed areas at higher energetic costs, this can create fragmented, isolated, and stressed populations, which can negatively affect metapopulation structure. The results are potentially high risks to bear population persistence (Frankel and Soulé 1992, Craighead and Vyes 1996, Paetkau *et al.* 1998, Waits *et al.* 1999).

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Conflicts with humans, hunting, and illegal commerce in bears and bear parts are also prominent factors threatening sun bear survival in many areas, particularly in mainland Asia (Mills & Servheen 1994, Meijaard *et al.* 2005). This is becoming especially problematic for Indonesian sun bears because the decline of bear populations from hunting and habitat loss in Malaysian Borneo and mainland South-East Asia may provoke a shift in demand to Indonesian sun bear populations for body parts for Asian medicines and cosmetics, as well as for live bears.

Despite the sun bear's legal protection internationally, as well as in Indonesia and Malaysia, hunting and commerce are increasingly significant threats to its survival. Results from interviews with regional and village heads and traditional leaders throughout the study sites indicated concerted interest each year to hunt bears for body parts or meat, to reduce fear of attacks, to take bears for the pet trade, and to kill bears as perceived pests. Current take levels are high compared with previous years and may validate assumptions that a market for bears and bear parts is rising in Indonesia (Meijaard *et al.* 2005). The increasing transportation by rivers, light planes, and the network of legal and illegal logging roads and subsequent spur roads, trails, and forests opened by logging increase access for hunters. With enhanced access to outside markets and exports, such hunting pressures on a population already considered to be reduced by over 75% across its range (Servheen 1999a) can result in significant strain on the species. With the combined impact of habitat loss and fragmentation, continued hunting can reduce the population to unrecoverable levels.

In Indonesia the more immediate threats to sun bear persistence are currently forest loss and disturbance. In addition to increasing bear mortality from losses in forage and other vital resources, habitat loss also increases hunter access as well as the likelihood of chance interactions and conflicts with people on the edges of reserves (Fredriksson 2005), during or after which bears are inevitably killed.

On a community level, altering the bear's geographic ecology can shift the structure and dynamics of bear sub-populations, which can affect community-level dynamics, such as competition, seed dispersal, and predation (Augeri 1994, 1995). For example, based on observed sign characteristics and their associated activities, it is clear that sun bears provide specific functional roles for their surrounding ecological communities (table 8.1). Fruit consumption was the most frequently observed sign and scat contents and, thus, seed dispersal, which is important for forest regeneration, persistence, and evolution, can be considered a prominent functional role of sun bears for the ecosystem. Other essential needs for forest dynamics are soil mixing, aeration, biomass breakdown, and nutrient enhancement, all of which sun bears provide while foraging on termite and ant colonies and other soilbased resources (e.g. beetles, logs, small mammal burrows), in addition to digesting and then recycling waste products back into the system. For example, nitrogen isotope tagging and other studies in north-west North America showed that the actual nutrients digested by bears from eating salmon on the coast were deposited hundreds of metres inland and were absorbed by the surrounding floral community, including in mature trees, shrubs, herbs, and mosses as well as in insects and birds (Gende *et al.* 2002, Hocking and Reimchen. 2002, Bilby *et al.* 2003, Moola *et al.* 2004). As an important competitor and predator across the tropical forest community, sun bears also provide necessary functional effects on system dynamics, such as agonistic, competitive, and demographic influences.

Table 8.1. Examples of principal sun bear signs observed with associated activities and related ecological roles those activities provide for the sun bear population in general and surrounding tropical forest community.

Observed Sign	Associated Activity	Related Ecological Function
Climbing for Fruit, Scat Contents, Discarded Fruit	Fruit / Nut Consumption	Seed Dispersal / Predation / Competition
Bee hive tearing	Bee Hive Consumption	Predation / Cavity Creation
Termite Colony Tearing	Termite Consumption	Predation / Nutrient Mixing / Competition
Scat Contents	Vertebrate Consumption Insect Consumption Plant Consumption	Predation and Competition / Nutrient or Biomass Breakdown
Log Tearing	Insect foraging	Predation and Competition / Nutrient or Biomass Breakdown and Mixing
Digging for Forage (with spoor sign)	Foraging, "Rooting" and Plant Consumption	Predation / Soil and Nutrient Mixing / Herbivory
Nests (with hair)	Nest Building/Tree Cavity	Shelter for many species and biomass breakdown
Claw Marks	Territorial Marking	Competition / Mating Signals
Spoor and Sightings	Foraging / Immigration and Emigration / Dispersal / Territorial & Transient Ranging	Predation / Agonistic and Competitive Pressures / Demographic Shifts / Competition and Foraging

If these activities are disrupted by human activities, resource loss, or habitat fragmentation, this can alter the bears' movement patterns across the landscape and their access to primary resources. Over time, this can potentially impact the bears' ecological roles, which can affect the demography, density, and dynamics of surrounding flora and fauna communities. Ultimately, important implications for sun bears and tropical biodiversity are inevitably linked to scientifically-sound forest conservation planning, such that the persistence of local sun bear sub-populations depends on:

- (1) Predicting how biogeography, changing landscape structures, environmental stochasticity, and other anthropogenic disturbances, including hunting, affect bear movement and foraging patterns across time and in increasingly patchy landscapes.
- (2) Facilitating increased access for bears to available critical resources and habitat over the long-term.

Sun bears in these study sites are clearly an interior forest-dependent species with a strong affinity for undisturbed mature, diverse, and heterogeneously-structured primary forests. Abundance estimates indicate population sizes are low and seriously threatened and both legal and ethical guidelines dictate that a network of large protected primary forest reserves, with adequate buffer zones and corridors, are necessary for population persistence in Indonesia. Given that Borneo and Sumatra each harbour the most continuous sun bear populations remaining across its range, Indonesia can be considered the central and most important foundation for the species. In this light, a metapopulation approach to global sun bear management is recommended.

Currently, the global sun bear population is highly fragmented in an archipelago of isolated protected and unprotected forests across South-East Asia. Most of these areas are small and are increasingly susceptible to encroachment and edge effects. Deforestation rates are rising throughout the bear's range, but enhanced conservation strategies are possible. Indonesia can play a pivotal role by (1) providing landscape-level protection of the largest remaining primary forests left in the region, (2) restoring degraded lands, and (3) implementing and enforcing strong conservation policies and protective mechanisms. Protected and restored areas are critical for conserving the genetic and demographic diversities of sun bears and can serve as a central reserve in the protective network across the bear's range in South-East Asia. Restoration of degraded or cleared areas provide important buffer zones and corridors connecting primary forest reserves within and between countries while also providing important ecosystem services and protection against natural disasters for local human communities. Given the bear's diverse niche and broad ranging patterns, managing forests for sun bear conservation will facilitate protection for a diverse array of tropical species and ecosystems, some critically endangered, and will provide important ecosystem services for surrounding human communities.

"If we pretend we are the center then we circle, dead moons... This morning I ask only to wear the skin of the bear in my songs..." Joseph Bruchac (1993)

8.2 <u>Conclusions</u>

This study has improved insights into the complex dynamics of sun bear habitat selection and how various biogeographic and disturbance factors affect their use of landscapes. Results demonstrated that sun bears are likely an interior forest-dependent species in these areas. In all sites and ecosystems on Sumatra and Borneo, mature interior forest characteristics were prevailing factors in sun bear habitat use, with 92.7% of observed bear activity in undisturbed forests. In these sites, tree species diversity, forage abundance, mature stand traits, and cover were the most important variables associated with 97% of bear habitat use. The presence of competitors and antagonistic species did not significantly affect sun bear habitat use geographically, but the presence of tigers may have had some temporal influence. Mature forest characteristics, especially a predominance of large mature fruiting trees, substantial escape cover, and high tree species diversity, were the most outstanding factors associated with the bears' habitat use in undisturbed areas and are potentially important indicators of interior forest affinity for bears. These habitat characteristics were prominent influences on sun bear habitat use patterns in undisturbed areas, but habitat disturbance and human activities were the most profound and overwhelming influences on sun bear habitat use and possible movements, densities, and distributions across these sites.

The direct and interactive effects of habitat disturbance on sun bear ecology and landscape use were consistently the most significant effects across all other variables, regardless of habitat type, ecosystem, biogeographic condition, site, area, or region. The type, intensity, age, and geographic extent of disturbances accounted for the significant majority of the variance in sun bear habitat use. Human activities were also important, indicating that a form of virtual fragmentation may occur in some areas, but the most significant effect was the interaction between the age of, and distance to, intensive forest clearing relative to where and when bears were active. Edge effects were a central influence, in which sun bear habitat use rose significantly as distance from disturbance increased, and habitat use did not reach consistently high levels until > 10 km from the disturbance. Overall, sun bears appear to be choosing cover and security over food. For most bears, any notable loss of this resource will reduce their reproductive success and persistence.

Bear activity in secondary forests and post-disturbed areas was insignificant by relatively few bears in those populations and was directly correlated with the age of the

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disturbance. The later the stage of succession in regenerating forests, the more those areas were used by bears. Only a low to moderate amount of bear activity was observed in secondary forests that at least retained some of the mature forest structure that is characteristic of more frequently-used sites, and only once stands had regenerated > 25 - 30 years. Observations of sun bears using post-disturbed forests should be considered relative to forest age and frequency of use by bears relative to the number of bears in that population.

This is the first study of its kind for the sun bear that has generated empiricallybased density and abundance estimates, and the first study on bears using presence-absence site-occupancy models, such as those by MacKenzie *et al.* (2002) and Royle and Nichols (2003), integrated *via* methods proposed here. Results indicated that sun bear distributions are patchy and fragmented across the landscape matrix. Consistently occupied sun bear habitat is mainly in undisturbed primary forest, whereas bears avoid highly disturbed areas. Disturbance is creating both fragmentation of populations and possibly habitat compression that concentrates bears in smaller available habitat in remaining forest patches and reserves.

Habitat compression may be inducing density-dependent spatial patterning among bears in small forest patches and habitat "island" reserves and, subsequently, aggregating bear activity. Although sun bears are randomly distributed within undisturbed primary forests, they are clustered or "compressed" in secondary forests and in sites affected by disturbance. Due to loss of suitable habitat, sun bear ranges are highly fragmented across the overall landscape. Populations appear to be fragmented between occupied forest sites, where most occupied areas are in large continuous primary forests in more remote locations at elevations of 400 - 1,000 m asl, with the majority > 500 m asl, probably due to high intensity disturbance and human use below 500 m asl. Actual sun bear ranges are probably limited to specific areas within undisturbed primary forest and older secondary forest (> 30 years old), and shift on a seasonal and annual basis.

Escalated hunting is having an increasing influence and may interact with forest loss to reduce populations to unrecoverable levels, but deforestation and fragmentation are currently the most deleterious effects on sun bear persistence in Indonesia. This research supports the general theories and hypotheses described in Chapter 3 that habitat loss and fragmentation result in insularity, blocking the bears' ranging ability between suitable habitats, increasing pressures and stress on individual bears, and, subsequently, affecting overall population dynamics. As a result, small sub-populations will become seriously threatened and metapopulation persistence will decline.

The distribution of bear signs, photographs, and genetic samples in this study were suitable measures of the distribution of individuals when examined together in presenceabsence and multivariate models. The preponderance of these analyses indicate that in the majority of cases, (1) sign absence most likely indicated bear avoidance of those areas and (2) moderate bear activity was probably selection of specific sites. The strength of these analyses was, however, due to several fundamental components of the study design:

- (1) Stratified-random sampling with a large number of independent random samples in multiple habitats, ecosystems, and regions over multiple years, which reduced habitat, seasonal, and annual biases and individual variation and enabled more confident generalisations across these study sites.
- (2) Method plurality, testing, and redundancy, thereby reducing bias.
- (3) A two-staged nested-experimental design, which reduced statistical bias, violations of independence, and other confounding effects.
- (4) Tested habitat bias and sign aging, particularly relative to disturbance, human activity, and other factors like the presence of influential sympatric species, which reduced misleading extrapolations.
- (5) Extensive statistical modelling of multiple potential effects and their interactions, which reduced spurious conclusions of arbitrary effects.

The methods used to generate density and abundance estimates were tested and found to be sound, but results should be considered relative to model and method assumptions with associated error. Models indicated that the most densely-populated area in this study was Kayan Mentarang National Park ($\overline{x} = 0.0416$ bears/km²), followed by the Bulungan Ecosystem ($\overline{x} = 0.0246$ bears/km²) and then Gunung Leuser National Park ($\overline{x} =$ 0.0234 bears/km²). Given model assumptions and associated error and assuming some degree of overlap among adults, abundance estimates for Kayan Mentarang are about 582 – 873 adult bears. In the Bulungan Research Forest, there are about 104 - 156 adult bears and in Gunung Leuser National Park there are about 186 – 280 adult bears. These estimates are consistent with published densities for the sun bear's closest phylogenetic relatives Ursus americanus and U. thibetanus, as well as for U. arctos, Melursus ursinus, and Tremarctos ornatus (Powell et al. 1997, Servheen et al. 1999, Kattan et al. 2004). Tests show the data and models in these analyses are robust, but reported density and population figures should be viewed cautiously as estimates with associated error and assumptions. These estimates provide an initial baseline, which further research should validate by comprehensive multiyear mark-recapture studies in representative habitats and conditions across multiple sites.

Results indicate low sun bear population sizes in the largest protected areas in its global range. Until now, *Helarctos malayanus* has been listed as Data Deficient, but this research in its entirety provides sufficient information to update the IUCN Red List (v. 3.1)

for *Helarctos Malayanus* to Vulnerable (VU C2ai) in Indonesia and possibly to Endangered (EN, based on criteria B1bi-v, C2ai and D) or Critically Endangered (CR, based on criteria B1a and B1bi-v) in other regions where small and isolated populations occur (Chapter 7). These data also support the CITES Appendix 1 listing that *H. malayanus* is in danger of extinction and is or may be affected by international trade. The bear's strong affinity for primary forest and the increasing rate of forest loss throughout its global range suggest scientifically-based conservation measures should be implemented without delay.

A time-space mosaic can help planners create realistic and ecologically-sustainable reserve networks in increasingly-fragmented landscapes. Primary forests are needed to sustain the sun bear population and should be proportionally larger than all other landscape uses. Primary forest reserves should be $> 200 \text{ km}^2$ and should be connected to large protected areas $> 10,000 \text{ km}^2$. All protected areas should be surrounded by buffer zones > 5 km wide and corridors connecting reserves should be at least 8 - 10 km wide. Buffer zones can be secondary forests, but a minimum of 25 - 30 years are required for such forests to regenerate sufficiently to support bears at low to moderate levels, and primary interior forests need to be more than 5 - 10 km from major or intensive disturbances.

This reseach has provided (1) scientists with information to further clarify the complex dynamics of sun bear biogeographic ecology and (2) decision-making bodies with the necessary information for conservation planning. Several questions remain and I recommend that research and conservation work continue on sun bears in Indonesia and in other regions. In particular, biologists should specifically examine habitat fragmentation using empirically-supported models, along with how and where suitable corridors, reserve networks and core habitat patches in particular biogeographic configurations sustain adequate population viability. More detailed reasearch through observation and radio-telemetry is needed on sun bear life history and its ecological relationships in forest systems. Such research will lead to sound conservation planning initiatives for sun bears, biodiversity, and tropical forests. Hence, many other threatened and endangered species will be protected.

During this study several collaborative research and conservation projects were developed with Indonesian-based organisations, and some of these projects will continue on sun bears and other species, including work focused on highly endangered species such as Sumatran tigers and elephants. Conservation planning and education were also initiated with some groups, and with local communities adjacent to these study areas, but these were only initial efforts based on minimal funding. More work and funding are needed, along with partnerships to develop comprehensive multi-party initiatives that ensure the implementation of long-term scientifically-based conservation plans for sun bears and tropical forests.

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APPENDIX I

EXAMPLES OF CAMERA-TRAPPING PHOTOGRAPHS OF BEARS AND SYMPATRIC COMPETITOR AND ANTAGONISTIC SPECIES





Figure A1. Malayan sun bears (*Helarctos malayanus*) in Kayan Mentarang National Park.



Figure A2. Sumatran tigers (Panthera tigris sumatrae) in the Leuser Ecosystem.





Figure A3. Clouded leopards (*Neofelis nebulosa*). Top: Kayan Mentarang National Park. Bottom: Leuser Ecosystem.





Figure A4. Asiatic golden cats (Felis temninckii) in the Leuser Ecosystem.





Figure A5. Top: Bay cat (*Felis bada*) in Kayan Mentarang National Park, which is the first known photo of this species, taken on 5 June 2003. Bottom: Marbled cat (*Pardofelis marmorata*) (far right-center on log) in the Bulungan Research Forest.



Figure A6. Top: Banded linsang (*Priondon linsang*) in the Bulungan Research Forest. Bottom: Leopard cat (*Felis bengalensis*) in Kayan Mentarang National Park.





Figure A7. Top: Bearded pig (*Sus barbatus*) in the Bulungan Research Forest. Bottom: Eurasian wild pig (*Sus scrofa*) in the Leuser Ecosystem.



Figure A8. Asian elephants (*Elephus maximus*) in the Leuser Ecosystem.



Figure A9. Top: Pangolin (*Manis javanicus*) in the Bulungan Research Forest. Bottom: Binturong (*Arctictis binturong*) in the Leuser Ecosystem.





Figure A10. Top: Malay civet (*Viverra tangalunga*) in Kayan Mentarang National Park. Bottom: Yellow-throated marten (*Martes flavigula*) in Kayan Mentarang National Park.





Figure A11. Top: Pig-tailed macaque troop (*Macaca nemestrina*) in Kayan Mentarang National Park. Bottom: Hose's langur (*Presbytis hosei hosei*) in Kayan Mentarang National Park.



Figure A12. Top: Sambar deer (*Cervus unicolor*) and bottom: yellow muntjac (*Muntiacus atherodes*) in the Leuser Ecosystem.



Figure A13. Top: Lesser mouse deer (*Tragulus javanicus*) in the Leuser Ecosystem. Bottom: East-Asian porcupine clan (*Hystrix brachyuran*) in Kayan Mentarang National Park.



Figure A14. Great argus pheasant (*Argusianus argus*) in Kayan Mentarang National Park. Bottom: Crested fireback pheasants (*Lophura ignita nobilis*) in the Bulungan Research Forest.

APPENDIX II

SUN BEAR HAIR AND SCAT GENETIC SEQUENCES

Mitochondrial Sequencing Data

<u>Sun Bear ID SB1 – (lab sample L2 hair) – (*Helarctos malayanus*) – exact match with L3 hair</u>

ACATCCCATGGGCCCGGAGCGAGAAGAGGGTACACGTACCCGCAAGGGTTGCTG GTTTCTCGAGGCTTGGTGACCAAGCTCCCGGACTAAGTGAGATACATATCTACA GACTATACACCTAAAACAAGCTTTTGGAATGTAGGTCCTCATGTAAGGCCAAGC ACAATATGTACATGCTTATATGCATGGGGGCACACCATTAATGCACGACGTACAT AGGGGGGAAAAAAAATAAAAGAGGGAGTACTTGAAAACATACTACGATGGCAC AGTACATGGAATGATATATATGAAATAAATAGGGCATTGGGTGGAATAGCGGTA TGTACCAAGGAATAGTTTAAATAGAACATCAGCTTTGGGTGGCACT

<u>Sun Bear ID SB1 (lab sample L3 hair) – (Helarctos malayanus) – exact match with L2 hair</u>

Sun Bear ID SB2 – (lab sample T2 scat) – (Helarctos malayanus)

Sun Bear ID SB3 - (Lab sample L1 scat) - (Helarctos malayanus)

TATAGTTCCAACATAGAAACCCCCACATCCCATGGGCCCGGAGCGAGAAGAGGT ACACGTACTCGCAAGGGTTGCTGGTTTCTCGAGGCTTGGTGATCAAGCTCCCGG ACTAAGTGAGATACATATCTACAGGCTATACACTTAAAACAAGCTTTTGGAATG TAGGTCCTCATGTAAGACCAAGCACAATATGTACATGCTTATATGCATGGGGCA CACCATTAATGCACGACGTACATAGGGGGGGAAAAAAAATAAAAGAGGGAGTA CTTGAAAACATACTACGATGGCACAGTACATAGAATGATATATAGAAATAAAC AGGGCATTGGGTAGAATAGCGGTATGTACCAGGGAATAGTTTAAATAGAACATC AGCTTTGGGT

Sun Bear ID SB4 – (lab sample L5 scat) – (Helarctos malayanus)

Sun Bear ID SB5 – (lab sample L8 scat) – (Helarctos malayanus)

Lab sample K1 hair - Felid