POPULATION STATUS OF TIGERS (*PANTHERA TIGRIS*) IN A PRIMARY RAINFOREST OF PENINSULAR MALAYSIA

By

KAЕ KAWANISHI

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POPULATION STATUS OF TIGERS (PANTHERA TIGRIS) IN A PRIMARY RAINFOREST OF PENINSULAR MALAYSIA

By
Kae Kawanishi

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Chair: Melvin E. Sunquist
Major Department: Wildlife Ecology and Conservation

Ecology and conservation of tigers (Panthera tigris) are least known from the Indochinese region largely due to the difficulty of studying elusive, forest-dwelling animals that occur naturally at low densities. The paucity of basic information is a major obstacle to developing an effective conservation strategy in this region. Using camera-trapping techniques and capture-recapture population estimation models, this study provided the first statistically valid model-based density estimates of tigers in Taman Negara National Park, the most important conservation area in Peninsular Malaysia. Three study sites of approximately 200 km² each in the lowland primary rainforest were sampled between 1999 and 2001. It took over 14,000 trap nights to accumulate 35 photographic captures of tigers or 61 tiger photos, which constituted 1.3% of the total wildlife photos. Estimated densities (X ± SE) of adult tigers ranged from 1.10 ± 0.52 to 1.98 ± 0.54 tigers/100 km². The differences were not significant (X² = 1.56, df = 2, P = 0.46) with the overall mean estimate of 1.66 ± 0.21 tigers/100 km² (n = 3). The tiger population in the park was roughly estimated to be 68 (95% CI: 52-84) adult tigers or 91 (95% CI: 70-112) adults and cubs. No evidence of poaching of large mammals was found in the study sites. At the perceived minimal level of poaching, the Taman Negara’s tiger population appears to be viable for at least...
100 years. The photographic data were used to make a crude inference on available prey biomass. The estimates ranged from 266 to 428 kg/km$^2$, and wild boars ($Sus scrofa$) were the most important potential prey species in both abundance and biomass. Although the method to estimate prey biomass was crude with the underlying assumptions untested, the result was as expected of a typical primary rainforest. Three major sources of possible human impacts on the tiger-prey community in Taman Negara are aborigines, tourists, and poachers. A negative correlation between level of human traffic and abundance of large mammals was observed, but overall impacts on the tiger-prey community appear to be minimal in Taman Negara as a whole.
CHAPTER 1
INTRODUCTION

The tiger (*Panthera tigris*) has lost more than 95% of its original range in the past century. The current continental distribution of tigers extends from the boreal forest of the Russian Far East to the tropical rainforest of Malaysia, covering 12 East to South Asian nations. In Indonesia, the only extant population of tigers is on Sumatra.

Tigers are a highly adaptable species and exhibit tolerance to a wide range of forest types, climatic regimes, altered landscapes, and prey bases (Schaller 1967, Sunquist et al. 1999). Their resilience, a product of adaptability and high fecundity, has allowed tigers to survive the massive onslaught and habitat loss of the past century. However, many of the remaining tiger populations are confined to small, isolated, less productive forests. While negative human impacts on tigers, their prey, and habitats continue, impending local extinction of isolated small populations, though they may go unnoticed, threatens the long-term survival of the species.

The ecology and conservation status of tigers are least known from the Indochinese region (i.e., Vietnam, Cambodia, Thailand, Laos, Myanmar, and Malaysia). This is largely due to the difficulty of studying elusive, forest-dwelling animals in regions marked by political instability and social upheavals over the past several decades (Rabinowitz 1999). The current knowledge of tigers in the region lags greatly behind that in India, Nepal, and Russia, where tigers have been studied for at least 4 decades and where tiger numbers in some areas appear to be recovering or stabilizing (Karanth et al. 1999, Smirnov and Miquelle 1999). Efforts are underway to increase our knowledge of the status of Indochinese tigers and some nations in the region have initiated scientific studies to acquire the information needed to develop sound conservation strategies (Rabinowitz 1999, Karanth 2001). Malaysia is one of these countries.
Malaysia occupies the southern limit of the distribution of the mainland tiger populations. Malaysia is divided into 2 regions: Peninsular (West) Malaysia, covering 131,700 km² of the Malay Peninsula, south of Thailand; and East Malaysia, occupying 198,300 km² of northern Borneo where tigers do not occur naturally. In the past century, Malaysia lost half of its forest cover and most of the remaining forests are located primarily in mountainous regions with little agricultural value or in isolated protected areas. Since independence in 1957, large areas of productive lowland forests in Malaysia have been converted to oil palm and rubber plantations through government agricultural development schemes. In addition to this habitat loss and fragmentation, increased demands on wild meat and high-priced body parts of some wild animals have reduced populations of many large mammals, including Asian elephant, sambar deer, gaur, tapir, Sumatran rhinoceros, and tiger. The Javan rhinoceros and banteng, species which had restricted distributions and small populations in the early 20th century (Hubback 1932), are now believed to be extinct in Peninsular Malaysia (Aiken and Leigh 1992).

With the opening of the forests for agricultural development and the raising of livestock, the natural habitats and prey most preferred by tigers were depleted and at the same time tigers began to prey on domestic animals. Consequently, up until 1970s, many tigers were killed as pests (Blanchard 1977, Khan 1987). The official persecution of tigers in most parts stopped in 1976 when the tiger became a totally protected species under the Protection of Wildlife Act of 1972. Anyone found guilty of killing a tiger is liable to a penalty of up to RM15,000 (US$4,000) and/or up to 5 years imprisonment.

The recent declines in tiger numbers across its range were also evident in Malaysia, where the estimated number of tigers declined from 3,000 in the early 1950s (Locke 1954) to 250 in the early 1980s (Khan et al. 1983). A more recent official estimate of 500 tigers (Khan 1987, Topani 1990), based on years of surveys and depredation reports verified by the staff of the Department of Wildlife and National Parks (DWNP), suggests a population comeback. Asserting
that the estimate was conservative, Khan (1987) adjusted the figure to be 600-650. This figure still serves as the current estimate (Samsudin and Elagupillay 1996).

The existing protected area system in Peninsular Malaysia relies heavily on its only national park, Taman Negara National Park. It was established between 1938 and 1939, and largely due to its inaccessibility, the park has remained intact and undisturbed. It encompasses 4,343 km$^2$, accounting for 59% of the total protected area in Peninsular Malaysia. It is not only the largest park among 13 national parks in the nation (12 other parks are in East Malaysia) but also one of the largest in Southeast Asia.

Taman Negara is part of a large contiguous tract of forest that stretches to southern Thailand. Encompassing a total of 27,469 km$^2$, this large forest tract includes 5 protected areas of 7,135 km$^2$ (Dinerstein et al. 1997). It thus offers the best chance for long-term viability of the tiger population in Malaysia, which is completely isolated from other continental tiger populations. The conservation significance of Taman Negara is not only geographical but also political. Under the Constitution of Malaysia, land is a state matter and the State Executive Committee of each state, not the Federal Government, is the highest decision-making body concerning land-use policy. Taman Negara represents the only large forested land (>1000 km$^2$) in Peninsular Malaysia that comes under direct jurisdiction of the Department of Wildlife and National Parks, and thus the Federal Government. Furthermore, about 30% of the remaining original lowland (<300m ASL) forest of Peninsular Malaysia are protected in Taman Negara. Therefore, in addition to tigers, Taman Negara is the last stronghold for many other endangered species in Malaysia.

Observations of tigers in rainforests are extremely rare. In addition to the inherent difficulty of observing cryptic, naturally low-density tigers, the nature of tropical forests hampers the direct observation, trapping, and radio tracking of rainforest tigers. The traditional approach to counting tigers based on tracks is also not reliable because of the unrealistic assumptions that 1) each individual tiger can be identified by its unique track shape and size and 2) track prints of
every tiger can be simultaneously found and recorded (Panwar 1979). It is possible to identify some tigers by their tracks left on a suitable substrate with experienced eyes (McDougal 1977), but suitable conditions are rare. Just finding tiger tracks in Malaysian rainforest is problematic. Furthermore, counting of subsamples requires an estimation of the detection probability for it to be a viable method to estimate the population size. In summary, population estimates based on subsamples of tracks lack statistical rigor, thus reliability (Karanth 1987, 1988).

Many of the earlier detailed ecological studies of tigers were conducted in tall grassland and deciduous forests of the Indian subcontinent (Schaller 1967, Seidensticker 1976, McDougal 1977, Sunquist 1981, Karanth and Sunquist 1985, and Smith et al. 1987) where capture and radio-tracking methods were feasible. Similarly, in the Russian Far East, some demographic information was obtained routinely from snow tracking (Matyushkin 1977) and foothold snares have proved effective for capture and thus radiotagging (Miquelle et al. 1999). The recent development of commercially available self-activating, remote-camera systems equipped with an infrared sensor has allowed researchers to look into the ecology of tigers in rainforest habitats (Griffiths 1994, Franklin et al. 1999, Lynam et al. 2001, O’Brien et al. in press).

Karanth (1995) pioneered the use of camera trapping in the framework of mark-recapture theory (reviewed by Nichols 1992) to estimate the tiger populations in India. The mark-recapture population theory was first developed to estimate populations of small mammals and birds that could be trapped, marked, released, and recaptured at relative ease. Since tigers have individually unique natural stripe patterns (Schaller 1967, McDougal 1977, Karanth 1995), there was no need to actually capture and mark sample animals. Karanth and Nichols (1998, 2000) applied this method to estimate tiger populations based on photographic captures at 9 sites in India using a program CAPTURE (Otis et al. 1978, White et al. 1982, Rexstad and Burnham 1991).

Applications of the earliest mark-recapture model for closed populations, the Lincoln-Petersen model, were limited by its restrictive and unrealistic assumption of equal capture probabilities among animals. The original model has gone through considerable improvements.
The program CAPTURE is a collection of mark-recapture population estimation models that can account for heterogeneous capture probabilities due to individual, behavioral and temporal variations. The sampling method and analytical procedures to estimate tiger densities from camera-trapping data using CAPTURE program have been refined by Karanth and Nichols (1998, 2000) for applications in India where both tigers and prey are relatively abundant. Karanth and Nichols (1998) concluded that the technique was superior to any other methods for estimating an absolute abundance of a tiger population where density was >3 tigers/100 km$^2$. Whether this technique would work at extremely low tiger densities, as expected for tigers in lowland rainforest of Malaysia, was unknown.

Against this background, my study had the following objectives:

1. To investigate the feasibility of the camera-trap technique and refine the sampling methods necessary to estimate the density of tigers in tropical rainforests using camera traps in the mark-recapture framework.

2. To estimate densities of tiger populations at 3 sampling sites in Taman Negara National Park, Malaysia.

3. To investigate the predator-prey relationships by estimating biomass, occupancy and examining community structure and activity pattern of principal ungulate prey species.

4. To assess potential human impacts on the predator-prey community.

My hypotheses were as follows:

1. Tiger densities are positively correlated with prey biomass of the study sites.

2. Tiger densities in the primary rainforest of Malaysia are lower than those in grassland and deciduous forests of the Indian subcontinent.

In addition to the data primarily collected with camera traps, tracks were surveyed monthly at every camera-trap location and random points between camera traps. All signs of the *Panthera* species and human activities were also noted whenever encountered. These data provided indices for abundance of prey species and level of human traffic at the study sites. Chapter 3 presents the results of the objectives 1, 2, and 3; and Chapter 4 presents the results of the objective 4. See Appendix A for scientific names of all the vertebrate species recorded in this
study. Appendix B includes the results of the performance test of the 2 types of camera-trap systems used in this study.
CHAPTER 2
STUDY AREA

Taman Negara National Park (4°10’ - 4°56’N, 102°00’ - 103°00’E) is located in north-central Peninsular Malaysia (Figure 2-1). Encompassing 4,343 km$^2$, it is not only the largest national park in Malaysia, but also one of the largest parks in Southeast Asia. Altitudes in the park range from 70 m to 2,191 m ASL at the peak of Mt. Tahan. Malaysia has a tropical climate with wet, hot and humid conditions year-round and relatively little seasonal variation (Figure 2-2). Annual average relative humidity is 86% with little monthly change from 82% minimum to 92% maximum. Temperatures also vary little with monthly maximum temperatures of 30 °C to 34 °C and monthly minimum temperatures of 22 °C to 23 °C. Excessively high temperatures (>35 °C) are uncommon because of sea-breeze effects; no point on the long peninsula is > 160 km from the sea. Based on data collected at 3 weather stations around the park between 1999 and 2001 (Malaysian Meteorological Service, unpublished data) Taman Negara received an annual average of 2,500 mm precipitation. While there are no distinctive wet and dry seasons, rainfall is highest from November-February, when north-east winds from the South China Sea bring the monsoon (Figure 2-2). The forest type is broadly classified as a tropical evergreen moist forest, which ranges from lowland humid tropical forest to montane oak (Fagaceae) and ericaceous forests (Weber 1972, Whitmore 1984).

There is one 13-km-long road inside the park, resulting in a road density of 0.023 km/100 km$^2$, one of the lowest in the world. This road density provides great protection for wildlife but a logistical challenge for wildlife biologists. Furthermore, the park’s trail system is also limited, except for those leading to the peak of Mt. Tahan. Other trails are located near tourist facilities,
all of which are situated at widely separated locations along the park boundary. These logistic
limitations have resulted in fewer field studies being conducted in Taman Negara than in other
smaller and more accessible reserves in Malaysia (Marshall 1973). Outside general survey works
and observation notes, research on elephants (Olivier 1978, Kassim 1991, Stuwe et al. 1998),
guars (Ogilve 1954), and tapirs (Williams 1979, 1980) are notable examples of a few ecological
studies carried out on large mammals in Taman Negara.

Because Taman Negara is a national park, public access is considered important. The 4
entry points for tourists are Kuala Tahan (park headquarters), Merapoh (MP), Kuala Koh (KK),
and Tanjung Mentong. My sampling areas were at MP, KK, and Kuala Terengan (KT), which
was about 8 km upstream, about half an hour boat ride on the main Temberling River or a 13-km
hike on a trail from the park headquarters in Kuala Tahan (Figure 2-1). General characteristics of
the 3 study sites are summarized in Table 2-1. Corresponding to the altitudes, ranging from 70 m
to 898 m, the vegetation type was lowland-hill dipterocarp (Dipterocarpaceae) forest in all the
sites. Headwaters of major rivers draining into north-central peninsula originate in Taman
Negara. There are thus ample sources for water in the park and no point within the study sites was
> 1km from the nearest stream. Some streams do, however, become ephemeral during dry spells.
There were 5 known salt-lick sites in MP and 1 each in KT and KK. All the field stations for this
study were at or near tourist facilities. Thus, all study sites were used by some tourists. The
number of park visitors has been increasing annually and Kuala Tahan attracts the majority of the
tourists, with 55,673 visitors registered in 2000. In contrast, the number of visitors to Merapoh
and Kuala Koh in 2000 was 5,257 and 5,528, respectively (Department of Wildlife and National
Parks, Taman Negara, unpublished data). Therefore, the level of tourism was highest at KT due to
the proximity to Kuala Tahan, followed by KK and MP.

Tourism activities are concentrated around the lodges and facilities in or near the main
rivers for fishing, boating, and swimming, at observation platforms near salt licks, or on
designated recreational trails in the forest. Fishing is prohibited in MP. At both MP and KK the
trail system is limited to areas near the entry points at the park boundary. In contrast, a southern quarter of the KT study site contained some trails leading to a distant hide and caves.

Corresponding to the number of tourists, the number of DWNP personnel stationed at MP, KK, and Kuala Tahan is 8, 8, and 60, respectively. There is usually 2-4 DWNP staff at KT for law enforcement and trail maintenance. In addition, 7 anti-poaching teams, consisting of DWNP rangers and part-time workers, regularly patrol remote areas of Taman Negara.

The other main human activity in the park is that of aborigines. Taman Negara supports approximately 400 aborigines, locally called Orang Asli. The particular tribe of aborigines living in the park is known as Batek. They are nomadic hunters and gatherers who sometimes engage in economic or commercial activities such as trading non-timber forest products or guiding tourists at Kuala Tahan. Batek’s staple food source is tubers (yams) of the genus Dioscorea and fruits in season (van der Schot 1990). They use blowpipes, poison arrows, smoke, and digging to obtain wild meat. Possession of firearms is prohibited. The source of animal protein consists of small to medium-sized species such as primates, squirrels, birds, bird’s eggs, porcupines, bamboo rats, pangolins, turtles, and fish. Although this study did not directly assess the effect of Batek’s hunting habits on wildlife abundance, it is generally believed that large herbivores and carnivores are unaffected directly by the Batek’s hunting techniques (van der Schot 1990; pers. observation, this study). Primates are hunted by Orang Asli, and the population appears to be depressed in areas with aboriginal populations in Taman Negara (van der Shot 1986). A study of primates at 9 forest sites around Peninsular Malaysia found that despite the floristic richness of a lowland forest site in Taman Negara, all 6 species studied occurred at lower densities in Taman Negara than other lowland forests (Marsh and Wilson 1981 in Chivers 1990). Their study site in Taman Negara was part of the KT sampling site in this study where the largest population of Batek was observed. Some Batek live in a settlement provided by the government just outside Taman Negara and are only part-time forest dwellers. Thus, the exact number of Batek living in the park is difficult to determine, but there appear to be about 150-200 full-time residents. Van der Schot
(1990) observed that the Kuala Tahan area supported the largest Batek population by providing them with opportunities for cash income as guides and merchants for tourists. Based on my observations and interviews with Batek, it is possible that the KT study site may support up to twice as many Batek as does KK. MP supports none.

MP does, however, offer the best accessibility by vehicle with a main highway running parallel to the entire length of the western park boundary, including the study-site boundary (Figure 2-1). It is only 8 km from the main road to the park entrance at MP, on a hard-surface road that passes through an oil palm plantation and small orchards. The only road in the park is found in MP and it extends 13-km eastward into the park. The road is used primarily to transport climbers closer to the peak of Mt. Tahan. Access to this road is limited to vehicles belonging to DWNP and daily traffic volume is low at <10 vehicles/day. The gate at the entrance to the road is closed and locked at all time. Boats are not used in the MP region for transportation except for recreation and research.

Accessibility to KT and KK is limited but was improved recently with the completion of paved roads to the park entrances. The main mode of transportation at KT is by boat on the Temberling River. The paved road to the headquarters at Kuala Tahan was completed in 2001. Before this, the majority of tourists arrived at Kuala Tahan by 3-hour boat ride from Kuala Temberling boat jetty. In the KT area, 8 km north of the center of tourism, local people still use water taxis for transportation. The land cover immediately outside the KT boundary is a large secondary forest, part of which was being logged during the study period. There are a few small villages (< 1,000 people) along the Temberling River.

The entrance to KK is accessible from a main highway by vehicle over 40 km of paved road that winds through a large oil palm plantation. There is a security check station at about the mid-point of the road. Oil palm plantations in this area are the largest among the 3 study sites and some forests near Taman Negara were cleared in the past 15 years to expand the plantation. The land use pattern outside the KK boundary is oil palm plantation and secondary forests that were
partly logged during the study. Boats are used by *Orang Asli*, park staff, researchers and fishermen, all depending on the water level. There are no townships in this area except for settlements (estate) inside the plantations.
Figure 2-1
Location of the 3 study sites, Merapoh, Kuala Terengan, and Kuala Koh in Taman Negara National Park in Peninsular Malaysia.
Figure 2-2
Monthly average temperature (line) and rainfall (bar) with a standard deviation (error bar) in Taman Negara, Malaysia. Data are collected from 1999 to 2001 at 3 weather stations nearest to the study area by Malaysian Meteorological Service.

Table 2-1
General characteristics of the 3 study sites in Taman Negara, Malaysia.

<table>
<thead>
<tr>
<th>Study site</th>
<th>Merapoh</th>
<th>Kuala Terengan</th>
<th>Kuala Koh</th>
</tr>
</thead>
<tbody>
<tr>
<td>Area sampled (km²)</td>
<td>200</td>
<td>200</td>
<td>200</td>
</tr>
<tr>
<td>Vegetation</td>
<td>Lowland-hill dipterocarp</td>
<td>Lowland-hill dipterocarp</td>
<td>Lowland-hill dipterocarp</td>
</tr>
<tr>
<td>Elevation (m ASL)</td>
<td>90 - 714</td>
<td>70 - 706</td>
<td>70 - 898</td>
</tr>
<tr>
<td>Stream density index (%) a</td>
<td>100</td>
<td>100</td>
<td>100</td>
</tr>
<tr>
<td>No. known salt licks</td>
<td>5</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>Road (km)</td>
<td>13</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>No. annual visitors b</td>
<td>5,257</td>
<td>55,673 c</td>
<td>5,528</td>
</tr>
<tr>
<td>Estimated no. aborigines d</td>
<td>0</td>
<td>100 - 133</td>
<td>50 - 67</td>
</tr>
</tbody>
</table>

a Proportion of 1-km² grid with streams on topographic map. Some may be ephemeral during dry spell.
b Registered tourists in 2000 (Department of Wildlife and National Parks, Taman Negara, unpublished data).
c Registered tourists in Kuala Tahan, the park headquarter, 8 km downstream of Kuala Terengan. Exact number of tourists visited Kuala Terengan is unknown.
d ven der Schot (1990) and personal observation, this study.
CHAPTER 3  
POPULATION STATUS OF TIGERS IN TAMAN NEGERA NATIONAL PARK, PENINSULAR MALAYSIA

Methods

Field Sampling

The general sampling design and statistical analyses used to estimate tiger density based on photographic capture data follow Karanth and Nichols (1998). Some modifications to the sampling design were necessary, as presented below, to fit the local conditions. Two types of remote camera systems were used in this study: TrailMaster® active infrared system (Goodson Associates, Inc., Kansas, USA) and CamTrakker® passive infrared system (CamTrak South, Inc., Georgia, USA). Detailed information on the specification of the camera models and set-up configuration is provided in Appendix B.

Following preliminary surveys and interviews with park rangers and aborigines regarding where tigers were known to occur in the park, 3 study sites were chosen. An area of approximately 200 km² was to be sampled at each site; a sample area of this size was judged sufficiently large to encompass the home range of several tigers. The 3 sites—Merapoh (MP), Kuala Terengan (KT) and Kuala Koh (KK)—were sampled between April 1999 and May 2000, March 2000 and January 2001, and October 2000 and August 2001, respectively. The ultimate goal of the camera-trapping was to maximize the capture probabilities of tigers, and camera systems were placed at strategic locations beside active game trails with an average spacing of 1 unit every 4 km². Care was taken not to leave a sufficiently large hole without camera traps where a tiger might have a zero capture probability. Trapping locations were by default stationary throughout the sampling period, but camera traps were occasionally moved to nearby areas with
fresh tiger sign or shifted to a new location if preliminary results revealed poor animal traffic at the particular site. GPS coordinates of all trap locations were recorded and plotted on maps.

The major constraint in this study was limited mobility. Except for a 13-km stretch of road at Merapoh (MP), there were no roads in the park and it usually took 6 to 8 weeks of actual field time, sometimes stretching to over 3 months, to “fill” the 200-km$^2$ sampling area with camera traps, and also to concurrently survey the area and check cameras set earlier. Generally, each trap location was visited for maintenance and data retrieval only once a month. This was a major difference between my study and that conducted by Karanth and Nichols (1998), where transportation by vehicles allowed traps to be checked daily.

Another difference from the earlier study in India was in the total sampling periods. To use the CAPTURE to estimate numbers of tigers using closed population models, sampling had to be conducted in a relatively short period. The maximum sampling period in the Indian studies was 3 months (Table 1, Karanth and Nichols 1998). In my study, 3 months would just allow us to complete deploying cameras in an entire study site, during which cameras set in the first months would have gone through 3 sampling sessions. Due to the naturally low-densities and/or low capture probabilities of tigers in the sampling area, it took 10 to 13 months to accumulate the requisite data at each site. Details of the sampling effort and tiger capture records at each site are presented in Table 3-1.

For individual identification both flanks of each animal had to be photographed simultaneously. This was achieved by setting up 2 cameras, 1 opposite the other, at points along both sides of suspected tiger trails or rarely by tigers voluntarily turning around in front of a camera. Only photographs in which individuals could be clearly identified were used for analysis. As a result, 3 of 38 capture photos had to be discarded (Table 3-1).

In addition to photographic data, any secondary signs (e.g. tracks, scrapes) of all large predators (i.e., tigers, leopards, and dholes) were recorded whenever encountered and large fecal samples (maximum diameter of >25mm) were collected, dried and stored for analysis. Signs of
rare species such as rhino sambar deer, and gaur, and sighting of any large mammals were always recorded. Signs of other mammals, however, were noted only when new areas were surveyed for the first time. Furthermore, 100-m-long transects on the ground in front of all camera traps and at random points between camera traps were surveyed for animal tracks every month. The random points between camera traps changed monthly and only relatively fresh tracks (<1 month old) were recorded.

Data Analysis

All statistical tests except for those in the program CAPTURE (see below) were performed using SPSS version 9.0.0 (SPSS, inc. Chicago, Illinois, USA). To standardize the terminology used in my analysis of camera-trap data, the most important and frequently used terms are defined as follows:

- **Trap night**: a 24-hour period during which a camera-trap was functional.

- **Detections**: total number of trap nights any given species was detected at each trap location. Therefore, the maximum number of detections per species per trap location per night is 1.

- **Tiger photos**: number of photographs of tigers excluding duplicates of the same individual taken simultaneously in a dual-camera setup.

- **Tiger detections**: total number of trap nights tigers were detected at each trap location. Note that individual recognition is not important.

- **Tiger captures**: total number of trap nights tigers with known identity were detected. The maximum number of captures of an individual tiger per night is 1, regardless of how many times it is detected at other trap locations.

- **Effective tiger captures**: total number of tiger captures exclusive of those occurring during the same sampling occasion. Thus, effective capture of each individual animal is either 0 (not captured) or 1 (captured) per sampling occasion. See below, CAPTURE, for “sampling occasion.”

- **Sampling period**: total length of time cameras were deployed in each sampling site.

- **Sampling session**: period between setting up and checking a camera trap at each trap location, usually 30-35 days.

**CAPTURE.** Following the analytical procedure described by Karanth and Nichols (1998, 2000), the program CAPTURE (Otis et al. 1978, White et al. 1982, Rexstad and Burnham 1991)
was used to estimate the abundance of tigers at 3 study sites. The program estimates abundance of closed populations. Thus, assumptions of geographic and demographic closure had to be met. Since camera trapping is a non-invasive sampling method, I assumed that the sampling technique did not affect the survivorship of animals. In many studies demographic closure can be met or at least approximated, but geographical closure is difficult to attain (Wilson and Anderson 1985). At least some portions of the boundary of all the sampling sites extended to a much larger contiguous forest block. Although closure is better assessed from a biological basis (Otis et al. 1978), a statistical test for closure is provided by CAPTURE.

CAPTURE is the most versatile collection of models for closed population estimation that can account for variable capture probabilities due to individual heterogeneity (model $M_h$), behavioral response (model $M_b$), or temporal variation (model $M_t$). Combinations of these 3 sources of variation in capture probabilities make up 7 possible models for population estimation (i.e., $M_{hh}$, $M_{hb}$, $M_{bh}$, $M_{tt}$, $M_{tb}$, $M_{th}$, $M_{bb}$) and a null model ($M_0$) with homogeneous capture probability. Computation of the estimator under the most complicated model $M_{tbh}$ is available by Lee and Chao (1994). CAPTURE uses a discriminant function model selection algorithm to provide an objective criterion for selecting the best approximating model. Then the population size ($N$) and standard error of the population size estimate [$SE(N)$] are estimated for the most appropriate model. In this study, however, due to small sample sizes, selection criteria were defaulted to the null model $M_0$ or model $M_h$ with minimum number of parameters involved. The population size estimator of model $M_h$ is known to be robust to violation of underlying assumptions (Otis et al. 1978, Burnham and Overton 1979). Thus, I report population estimations under the model $M_h$.

Capture histories were constructed for each tiger identified. A matrix consisted of $i$ animals in rows and $t$ trapping occasions in columns. Because tiger cubs were never photographed, $i$ animals included only adult tigers. A special consideration for definition of trapping occasions was necessary. The trapping effort varied considerably across trapping
locations and over time because 1) it took 3 months to set all the traps, 2) camera-trapping performance was inconsistent depending on model of cameras used (Appendix B), and 3) cameras were visited for maintenance only once in every 30-35 days; thus, some were continuously functional while others ceased to function prematurely. Figure 3-1 shows the inconsistency in daily total trap-nights over sampling period at 3 sites. All study sites, however, showed a similar trend with 8-10 general peaks in daily total trap-nights that gradually increased and declined at the beginning and end of each sampling period, respectively. This periodicity was largely due to the frequency of the monthly maintenance trip. On average, there appeared to be 9 trapping sessions; thus, I decided on a total of 9 trapping occasions for all the sites. The total trap-nights at each trapping location was divided by 9 and capture history of $i$ tigers were noted on each occasion. The capture histories were tallied from all the trapping locations at each sample site to construct the final capture matrix. Each trapping occasion ($n = 9$) consisted of an average of 520 trap-nights, about 12 nights per trap. For example, consider a study site with 40 camera-trap locations that was sampled for 10 months. The total trap-nights at each trap location varied considerably. Trap #1 had a total of 90 trap nights, Trap #2 had 180 nights, Trap #3 had 30 nights, and so on. The total trap-nights at each trap location were divided by 9 occasions and tiger capture was noted on each occasion. To construct the final capture matrix, capture histories of individual tigers were compiled from the first occasion from each trap locations (e.g., first 10 nights from Trap #1, first 20 nights from Trap #2, first 3.3 nights from Trap #3, etc), second occasion from each trap, and so on until the 9th occasion.

**Density estimates.** To estimate the tiger densities at 3 sites, the abundance estimates based on CAPTURE were divided by effective trapping areas, $A(W)$, as follows:

$$
\hat{D} = \frac{\hat{N}}{A(W)}
$$

where $A(W)$ consisted of a buffer area of boundary width, $W$, surrounding the polygon enclosed by the outermost trapping locations (Karanth and Nichols 1998). First, all trap locations were
plotted on a map using ArcView 3.1 (ESRI, Redlands, California, USA), and traps on the perimeter were connected to form a trapping polygon at each site. Then a boundary width was added around the polygon to obtain the effective trapping area.

The calculation of buffer width for this study required a further consideration. A buffer width is a function of the home range size, density of animals, and trap spacing (Wilson and Anderson 1985). Dice (1938) proposed that the buffer width be half the average diameter of home range of the species. Trap spacing greatly affects the home-range size estimates based on capture data (Stickel 1954), but the effect is reduced for animals caught 6 or more times (Tanaka 1980). That no tigers were captured more than 3 times in this study suggested that buffer width estimation based on recapture data would be biased. Karanth and Nichols (1998, 2000) used half the “mean maximum distance moved (MMDM)” by tigers captured on more than 1 occasion to estimate the buffer width (Wilson and Anderson 1985). However, this method did not yield a buffer width that reasonably reflects the home range size of tigers in my study. The numbers of tigers recaptured at different locations were 3, 2, and 3 animals for the 3 sites. They were all recaptured once or twice at most. The estimated boundary width using the MMDM method was 1.62 km, which was comparable to the estimated $W$ for both Nagarahole ($W = 1.87$ km, tiger density = 11.5 animals/100 km$^2$) and Kaziranga ($W = 1.38$ km, tiger density = 16.8/100 km$^2$; Karanth and Nichols 1998, Table 4). These 2 areas represent the maximum for tiger densities throughout its range; thus, it is unlikely that the home range sizes of tigers in the primary rainforest of Malaysia are comparable to those in Nagarahole and Kaziranga. The estimated $W$ for this study was clearly underestimated due to the limited number of recaptures and the fact that a few animals were recaptured only in the vicinity of the original capture site (i.e., the negative bias induced by the trap spacing).

To estimate $W$, therefore, I took half the absolute maximum distance moved (AMDM) by tigers captured on more than 1 occasion at each site instead of MMDM, which has the tendency to underestimate $W$ when samples are small. A similar approach was taken for estimating tiger
density in a primary lowland forest of Sumatra (O’Brien et al. in press) where tiger recapture data were limited. Assuming that tropical tigers also have exclusive home ranges, their $W = 4.5$ km (O’Brien et al. in press) gave a home range estimate of 64 km$^2$, which, in turn, corresponded well with their tiger density estimate of 1.6 tigers/100 km$^2$. Where the boundary area included contiguous forest outside Taman Negara I included it in the effective trapping area; however, those adjacent habitat types that were unlikely to be used by tigers (e.g., open agriculture land) were excluded from the effective trapping area.

By using the AMDM instead of MMDM for $W$, the effective trapping area, $A(W)$, could not be estimated, but was treated as a known constant. Thus, for the associated variance of the density estimate, I used the variance estimated for the abundance in CAPTURE. This is likely to underestimate the variance of the density estimate, but I knew of no way to estimate a variance for AMDM.

Prey biomass. Forty-four large feces (>25 mm in diameter), presumably from Panthera species, were collected opportunistically in the park. Hair samples of potential prey species were collected from local zoos and Department of Wildlife and National Parks museum specimens to form a reference collection. Fecal samples were washed and hairs were examined under a compound light microscope to identify the prey species. Samples were also sent to the Wildlife Conservation Society (New York, USA) Science Resource Center for identification of the predators based on molecular analysis. The method involves isolating total genomic DNA from shed gut skin cells in the scat and then PCR amplifying and sequencing a portion of mitochondrial DNA with species specific primers that contain species specific sites. Limited sample size ($n = 3$ for tigers; $n = 4$ for leopards) did not allow the reconstruction of the food habits of the Panthera spp. or quantitative analysis of prey selection.

In the absence of food habits information for tigers from true rainforests, I assumed primary prey species of tigers in Taman Negara were ungulate species weighing more than 2 kg, but excluded Asian elephants and Sumatran rhinoceros. Whether tiger prey on tapir is an ongoing
topic of discussion (Holden and Martyr 1998, Kawanishi et al. 2002). There are, however, no reliable records of tigers preying on tapir, but the possibility could not be ruled out and tapir was initially included as a potential prey species.

Limited data on kills and feces reveal that tigers preyed on sun bear \((n = 3)\), cattle calf \((n = 1)\), and pangolin \((n = 1)\). Sloth bears, black bears, and brown bears, all much larger than sun bears, are reported as prey of tigers (Schaller 1967). Thus, sun bear was included in the prey biomass estimate, but cattle and pangolin were not because the former almost never occur in the park and photographs of the latter species were too few \((n = 6)\) to be included in the biomass estimate calculation (see below). In addition, pig-tailed macaque and the largest ground bird, great argus pheasant, were added to the list of potential prey because they were photographed frequently at all sites.

Line-transect sampling did not yield a large enough sample size to estimate prey abundance. I thus decided to try to use the photographic data to make a crude inference on available prey biomass. The analytical procedure described above for estimation of animal densities using program CAPTURE was applicable only for male sambar deer with antlers. Capture histories were constructed for stags that were individually identified based on shape and color of antlers and mains. Growth and shedding of antlers over time were taken into consideration. For all other large herbivore species, I used a relative abundance index based on camera-trapping data to estimate densities. For an index to reflect a true density, there needs to be a monotonic relationship between the index and actual density (Thompson et al. 1998). There is to date only 1 study that estimated densities of animals based on camera-trapping rates by calibrating the rates against independent density estimates. O’Brien et al. (in press) used density estimates from line transects for prey species and program CAPTURE for tigers to develop a regression analysis of the number of trap-nights required to photograph at least 1 individual conditional on species presence. They concluded that the number of photos gives a reliable index of density for tigers and their prey in the Bukit Barisan Selatan National Park in Sumatra. In an
absence of such calibration in this study, I chose to adopt the calibration derived by O’Brien et al. (in press) to this study. An untested assumption made for this analysis was that the relationship between photographic data and independent density estimates was comparable between the 2 studies conducted in Sumatra and Malaysia. Due to the untested assumption and no associated variances for the estimates, the inference made here is weak.

O’Brien et al. (in press) cautioned that the density estimation based on the line-transect sampling may underestimate group-living species if undercounts of groups occurred. Each detection in this study was also counted as 1 regardless of number of animals in the same frame. This raised a similar concern for underestimation of group-living species. Thus in an attempt to improve the biased estimate, the number of detections was multiplied by average number of group size. There was little information on average group size from the local forest except for elephants (Olivier 1978). Furthermore, opportunities for observation in this study were limited (e.g., $n = 2$ for elephants). Therefore, the information on average body weight and group size of each species used to estimate prey biomass was adopted from the literature (Table 3-2). For elephant, I used the mean group size of 3.59 (Karanth and Sunquist 1992) over 3.33 (Olivier 1978) because the observed number of groups was much greater in the former ($n = 46$) than the latter study ($n = 2$).

To derive a density estimate for an $i$th species ($D_i$) at each study site, I used an average of both linear and reduced major axis regressions presented in O’Brien et al. (in press). Notations improvised for this study are as follows:

$$
\hat{D}_i = \frac{e^{(106.8 - RAI_i)/59.8} + e^{(111.4 - RAI_i)/68.32}}{2}
$$

where Relative Abundance Index for $i$th species ($RAI_i$) is

$$
RAI_i = \frac{\sum_j m_j}{g_i \sum_j p_{ij}}
$$
where \( m_j \) is the total trap-nights at the \( j \)th trap location, \( g_i \) is an average group size for \( i \)th species and \( p_{ij} \) is a ‘detection’ for \( i \)th species at \( j \)th trap location.

**Estimate of proportional occupancy.** Proportion of each sample area occupied by tigers was estimated from observations of secondary sign and camera trapping data. Following the method described by Nichols and Karanth (2002a), proportional occupancy was operationally defined as proportion of sampling units containing evidence of tiger activity, and was estimated as

\[
\hat{\psi} = \frac{\hat{r}}{s}
\]

where \( \hat{\psi} = \) estimated proportion of area occupied, \( \hat{r} = \) estimated number of sampling units containing signs of tiger, and \( s = \) total number of sampling units sampled. The variance for the estimated proportion of area occupied was estimated as

\[
\tilde{\text{var}}(\hat{\psi}) = \frac{\tilde{\text{var}}(\hat{r})}{s^2} + \frac{\hat{\psi}(1-\hat{\psi})}{s}
\]

The number of sampling units containing signs of tiger, \( r \), was estimated using CAPTURE. See Nichols and Karanth (2002a) for the conceptual framework for this analysis.

First, the sample area was subdivided into a 5 km x 5 km grid, or a 25 km\(^2\) sampling unit. There were a total of 9 such grids covering the entire sampling area in each site. Each grid was sampled with camera traps and monthly surveys for sign, including track-count sampling on 100-m transects. To keep the population “closed” while accumulating sufficient number of recaptures, data from 5 consecutive monthly sampling occasions were used to construct a capture matrix. The matrix consisted of columns of sampling occasions and the rows of grid cells, in which sign of tiger activities was found during the sampling occasions.
Because grids were sampled with different sampling intensity in terms of total number of camera-trap nights and area covered by surveys, an estimation based on the null model ($M_0$) with homogeneous capture probability would be inappropriate. Thus, high selection criterion for $M_0$, possibly due to limited sample size was ignored, and a model with the second highest criterion was used for estimation. This procedure was repeated to estimate the site occupancy of leopard. For other species, including bear, wild boar, muntjac, sambar deer, gaur, elephant, and tapir, instead of the 25-km$^2$ grid size, a 3 km x 3 km grid or a 9-km$^2$ sampling unit was used to better reflect the smaller home-range sizes of these species. With the reduced grid size, there were 26 grids covering the sampling area in Merapoh, 24 in Kuala Terengan, and 28 in Kuala Koh. Because the majority of grids were sampled (25 grids in MP, 24 in KT, and 26 in KK), random sampling was not necessary.

**Activity patterns of tiger and leopard.** Lastly, the relation between predators and prey species in terms of activity patterns was investigated. The percent activity level was calculated based on pooled camera-trapping data from the 3 study sites, exclusive of photographs of the same species taken within 1 hour at the same trap location. The activity pattern and relative abundance of tiger and leopard were also compared to investigate the possible ecological separation of these sympatric large predators. All leopard photos ($n = 150$) were of melanistic animals; thus, not only was it impossible to identify individuals but sometimes identification of sex was also difficult. Following Karanth and Nichols (1998), captures per unit effort (CPU = no. detections in 100 trap nights) was used as an index of relative abundance. Relative Abundance Index (RAI) used in the estimation of the prey biomass is basically the same statistic as CPU except for the distinction between grouped and solitary animals.

**Results**

**Tiger Density**

A total of 61 tiger photos, representing 1.3% of all wildlife photos, was collected at the 3 study sites during a total of 14,054 trap-nights between April 1999 and August 2001. At Merapoh
(MP), Kuala Terengan (KT), and Kuala Koh (KK), 5, 5, and 6 individual tigers were captured 11, 9, and 15 times, respectively. It took 394, 539, and 323 trap-nights to obtain 1 tiger capture at MP, KT, and KK, respectively (Table 3-1). Over the course of study, camera trapping was successful in detecting all medium to large terrestrial mammals expected to occur in Taman Negara except for Sumatran rhino (Appendix A). A few tracks of rhino were recorded in all study sites, indicating an extremely low-density species.

The long sampling period at each study site raised a concern for violation of the closure assumption. Although Otis et al. (1978) cautioned that the test statistic of CAPTURE has little chance of rejecting closure in the case of small samples, at least no marked departure from the assumption was suggested by the test result (Table 3-3). The model selection algorithm of CAPTURE identified $M_0$ for MP, and $M_h$ for both KT and KK as the most appropriate models. Because of the robustness of the estimator under model $M_h$, and the desire to use the same model for all 3 areas, the population estimates computed under $M_h$ are reported and used for further analysis (Table 3-3). The estimated average capture probabilities per sampling occasion were consistent across study sites, ranging from 0.13 to 0.22. The estimated probabilities that a tiger was captured at least once over the sampling period were 0.71 for MP and nearly 1.00 for both KT and KK (Table 3-3). Estimates of tiger population sizes at MP, KT, and KK were 7, 5, and 6 animals, respectively. Coefficients of variation were relatively large, ranging from 27% to 47%.

The absolute maximum distances moved by tigers captured more than once were 6.05 km, 8.22 km, and 5.17 km for MP, KT and KK, respectively (Table 3-4). When half these distances were added to their respective outer camera-trap locations, the effective trapping areas ranged from 317 to 453 km$^2$. The estimated tiger densities at MP, KT and KK were 1.98, 1.10, and 1.89 tigers/100 km$^2$, respectively (Table 3-4). The hypothesis that these 3 samples came from 1 population was tested using program CONTRAST (Hines and Sauer 1989). The differences were not significant ($X^2 = 1.56$, df = 2, $P = 0.46$) with the overall estimated mean of 1.66 ± 0.21 (SE) tigers/100 km$^2$. 25
Prey Biomass

Of 44 large-diameter fecal samples, only 7 samples belonged to tiger or leopard. The tiger samples contained sun bear \( (n = 2) \) and cattle calf \( (n = 1) \). The 4 leopard samples contained wild pig \( (n = 2) \) and \textit{Macaca} spp. \( (n = 3) \); 1 sample contained both wild pig and \textit{Macaca}.

The photographic data and track-count data of large mammals (Appendix A) had a strong positive correlation at all the sites (MP: \( r = 0.67, P = 0.001 \); KT: \( r = 0.76, P < 0.0005 \); KK: \( r = 0.85, P < 0.0005 \)), suggesting that they could provide indices for relative abundance. The biomass of herbivores and other potential prey species in the 3 study sites was crudely estimated based on the photographic data, but it has to be emphasized that the inference made here is weak and requires caution for interpretation and further analysis. This is because untested assumptions had to be made to apply the results of other studies, notably of O’Brien et al. (in press) and Karanth and Sunquist (1992). Associated variances of the estimates are unknown and probably large.

The density estimates were based on an average of 2 calibration regressions presented in O’Brien et al. (in press). Estimates for sambar deer \( (3.22 \text{ animals/km}^2) \) and serow \( (0.23 \text{ animals/km}^2) \) in KK, for example, were clearly overestimates (Table 3-5). There were unusually high numbers of photographs of both species at this study site. All the serow photos \( (n = 43, \text{ compared to 1 and 8 for other study sites}; \text{Appendix A}) \) of 2 animals came from a single trapping location. Monthly track surveys confirmed that serow was unlikely to be present at other areas in the study site. Thus serow density was adjusted using 2 animals in the effective trapping area of 317.24 km\(^2\). Similarly, a large proportion of the sambar deer photos \( (86\% \text{ of a total } n = 293; \text{Appendix A}) \) came from 2 trap locations at the only salt lick in the study site. Using program CAPTURE, the population estimate under model M\(_5\) for male sambar deer with antlers was 15 animals (Table 3-6). Using a ratio of 3:7 for adult and yearling males to all others (Karanth and Sunquist 1992), an estimate of 50 sambar deer was reached. Therefore, the density estimate in the study site was 0.16 animals/km\(^2\) in contrast to the original 3.22 animals/km\(^2\). Using CAPTURE to estimate sambar deer abundance was not applicable to other study sites due to limited captures \( (n \)
The estimated total biomass of large herbivores at 3 study sites ranged from 2470 to 9339 kg/km$^2$, largely depending on the density estimates of elephant (Table 3-5). On average, 2 of the mega-herbivores species, elephant and tapir, contributed 93% of the wild herbivore biomass in the area. Elephant alone contributed about 75% of the herbivore biomass (Figure 3-2). Estimates of available prey biomass at 3 study sites were 1912, 1281, and 786 kg/km$^2$ inclusive of tapir, or 428, 348, and 266 kg/km$^2$ exclusive of tapir (Table 3-5). Because of the weak inference with no associated variance on the estimated prey biomass, the statistical power to test the hypothesis that the tiger densities are positively correlated with prey biomass was weak. Nevertheless, the positive relationship between the tiger densities and prey biomass (Figure 3-3) generally conformed to the a priori expectation.

**Proportion of Occupancy**

Estimated proportion of area occupied by tigers was 67% in MP, 78% in KT, and 78% in KK with no significant difference among sites ($X^2 = 0.17, df = 2, P = 0.92$; Table 3-7). Proportion of area occupied by leopards was 100% in MP and KK, and 78% in KT with no significant difference among sites ($X^2 = 0.30, df = 2, P = 0.86$). The difference between tiger and leopard at each site was also not significant (MP: $X^2 = 1.36, df = 1, P = 0.24$; KT: $X^2 = 1.0, df = 2, P = 1.0$; KK: $X^2 = 0.11, df = 1, P = 0.75$). Among ungulates, the highest occupancy rates were attained by muntjac at 100% in all sites, followed by wild boar ranging from 88% to 100%. The lowest occupancy was of gaur with 4% to 40%. In KT, sambar deer, gaur, elephant, and tapir all had lower occupancy compared to 100% occupancy of muntjac (sambar: $X^2 = 12.37, df = 1, P = 0.0004$; gaur: $X^2 = 25.62, df = 1, P < 0.00005$; elephant: $X^2 = 15.15, df = 1, P = 0.0001$; tapir: $X^2 = 4.03, P = 0.045$).
Activity Patterns of Tigers and Leopards

Based on the time of photographic captures, tigers and leopards were more diurnal than nocturnal and there was considerable overlap between the species (Figure 3-4a). Dhole was excluded from this analysis due to its limited sample size \( n = 9 \), but all dhole captures were registered between 0800-1900 h. The activity patterns of the *Panthera* species were more similar to those of crepuscular/diurnal species such as muntjac, mouse deer, and pig (Figure 3-4b) than to nocturnal species such as tapir and sambar deer (Figure 3-4c). Sample sizes for tiger, leopard, muntjac, mouse deer, pig, tapir, and sambar deer were 43, 140, 475, 94, 401, 376, and 179, respectively.

The relative abundance indices based on detections per 100 trap-nights for tigers and leopards are presented in Table 3-8. With an untested assumption of the 2 *Panthera* spp. having comparable capture probabilities, abundance of tigers and leopards were similar in all sites except in Merapoh where relative abundance of leopards was an order of magnitude higher than tiger and those of leopards in 2 other sites.

Discussion

Application of Camera-trapping Method to Estimate Tiger Density in Taman Negara

The camera-trapping sampling technique in the mark-recapture framework was successful in estimating tiger density in a large tract of primary rainforest in Malaysia. This study provides the first statistically valid model-based tiger density estimates from Malaysia. Efforts required to collect satisfactory data were, however, very large with an average of 4,685 trap-nights over 11 months per site, which is impractical to recommend for most applications. In comparison with the camera-trapping study in Pench National Park, India, where 5 individual tigers were captured 21 times during 788 trap-nights (38 trap nights/tiger capture; Table 1, Karanth and Nichols 1998), this study took on average more than 10 times the effort to yield comparable data (i.e., 5-7 tigers captured 9-15 times, or 402 trap nights/tiger capture; Table 3-1).
There was also a question of whether similar results could have been attained with much less sampling effort. To investigate this I ran CAPTURE with the same data in 2 different scenarios, asking whether similar results could be reached if 1) only 56% of the sampling efforts were expended, using the data from the first 5 occasions out of the total of 9, and 2) only 78% of the sampling efforts were expended, using the data from the first 7 occasions? The test results are presented in Table 3-9. First, in all cases the sample sizes were too small to test for heterogeneous capture probability, particularly the test of the null hypothesis ($M_o$) against the $M_h$ model with the more robust estimator (Otis et al. 1978). Secondly, the data from Kuala Terengan could not be analyzed since the first recapture occurred at the 9th occasion. Only removal methods (model $M_b$ and $M_{bh}$) are appropriate to a data set with no recaptures, but the KT data set had an increase in number of animals caught over the trapping occasions; thus, it was not suitable for the removal models, either (Otis et al. 1978). Thirdly, the results from Kuala Koh under the $M_h$ model showed different degrees of fluctuation depending on the amount of effort expended. Only the data from Merapoh showed some consistency over increasing trapping efforts. However, the results with 9 occasions were better than those with 7 occasions with smaller standard errors of the estimates and smaller differences in estimates between the 2 models ($M_o$ and $M_h$). Therefore, the large sampling effort was needed to achieve the objectives of this study.

Furthermore, the limited sample sizes in most cases did not allow the model selection algorithm of CAPTURE to provide an objective criterion for selecting the best approximating model, and $M_o$ or $M_h$ always had the 2 highest selection criteria (Table 3-3); thus, the more robust and realistic model $M_h$ was selected for this study. Model $M_h$ assumes that each individual animal has a unique capture probability that is unaffected either by the animal’s response to traps or time. This was a reasonable assumption for this study where the non-invasive camera-trapping method collected capture data of animals in a rainforest with little seasonal variation.

The limitations of small sample sizes were a natural consequence of studying difficult-to-detect, low-density animals in rainforest habitat. Different trap locations may have yielded higher
capture probabilities with less effort. The majority of sample sites were in restricted areas (DWNP/MOSTE 1987), off-limit to public use except for aborigines. The knowledge of the park staff regarding tiger whereabouts was limited to areas near the centers for tourism activities, and even recommendations from the aborigines sometimes did not yield satisfactory results in a given time.

As found by Karanth and Nichols (1998, 2000), tiger cubs had very low capture probabilities with no captures despite observations of their presence in the study sites. An observation was made very close to 1 of the camera traps on the paved road in the first study site. However, the trap only captured a few adults, suggesting that cubs may avoid cameras. Given that cubs were never captured despite the huge trapping efforts expended, the technique is applicable to estimate adult tigers only.

**Tiger Population in Taman Negara**

Even when employing probably the most effective method to detect the presence of a large rainforest carnivore within a large area, it took a huge effort to collect the small samples. That the estimates permitted only a weak inference was an inevitable consequence of the small samples. Abundance estimation of prey species was even more problematic because the mark-recapture models were not applicable. Due to the lack of data from local forests (i.e., independent density estimates, average weight and group size), the inference made on the prey biomass was admittedly even weaker with no associated variance for the estimate. Nevertheless, these weak inferences were still better than traditional guesstimates based on the assumption of total counts of individually identifiable secondary signs of animals. These weak inferences are the best and only ones currently available from tropical forests in Malaysia. The merit of the discussion below would be strengthened greatly by independent estimates of prey densities from future studies in the local forest.

Based on the density estimates, an attempt was made to estimate the tiger population in the entire park. Although the sampling sites were not randomly selected, the results suggested that
the samples were taken from 1 population that occupied the area. In addition, the total effective trapping area constituted approximately 30% of lowland to hill forest of Taman Negara. For these reasons, I assume that the sample population was a good representation of the population in the lowland to hill forest of Taman Negara. The highest elevation in all the study sites was 898 m. Therefore the mean density estimate of $1.66 \pm 0.21$ tigers/100 km$^2$ was extrapolated to the area below 900 m, which constituted 89.7% of the park. Thus, 90% of Taman Negara supported an estimated 65 (95% CI: 49 – 81) adult tigers. A further attempt was made to include areas above 900 m and cubs into the total population estimate. In a primary rainforest of Sumatra, Griffiths (1994) found that the tiger density in montain forest above 1700 m was about half of that of lowland forest below 600 m. A demographic model of wild tiger populations suggests that cubs may form ~ 25% of a ‘normal’ tiger population (Karanth and Stith 1999). Assuming that tigers existed above 900 m at a reduced density of 0.83 tiger/100 km$^2$, and that 25% of the population consisted of cubs, the entire park could support 91 (95% CI: 70 – 112) tigers or 68 (95% CI: 52 – 84) adult tigers.

In the mid-1980s, Malaysia’s Department of Wildlife and National Parks (DWNP) estimated the tiger population in Taman Negara at 72 animals (Khan 1987). The estimate was based on the size difference of tiger tracks surveyed by DWNP staff over the years. Although the 2 studies used completely different sampling approaches, the estimates were similar with the DWNP estimate included within the 95% confidence interval of the estimate of this study. Because the former estimate lacks the statistical confidence, no direct comparison of the 2 estimates is possible and any observed difference is likely a consequence of sampling variation and the different sampling approach than a true difference in the population size. Thus without a measure of confidence, the point guesstimate of this nature, no matter how ‘official’ it may be, cannot be used to monitor the changes in population sizes. The study provides the benchmark density estimate against which future monitoring can be compared.
Several pieces of auxiliary information and sighting of cubs in the park suggest that the tiger population in Taman Negara is probably stable and at or near equilibrium. The information includes no record of a tiger being poached inside or in the vicinity of Taman Negara between 1986 and 2002; that this study found no signs of poaching of large mammals inside the park between 1998 and 2001; and 7 patrol units organized by DWNP and operating in Taman Negara recorded no poaching of tigers between 2000 and 2002 (IRF 2002). Thus, poaching of tigers and large mammals in Taman Negara appears to be negligible.

There are 2 other reliable estimates of tiger density from primary rain forests. Using estimated home-range size based on photographs from camera-trapping and observations of tracks, Griffiths (1994) calculated the tiger density in the primary lowland forest (<600 m) of the Gunung Leuser National Park (GLNP) in northern Sumatra to be 1.65 tigers/100 km². Another estimate based on camera-trapping data using CAPTURE was 1.56 ± 0.43 tigers/100 km² in a lowland forest (<500 m) of Bukit Barisan Selatan National Park (BBSNP) in southern Sumatra (O’Brien et al. in press). The overall mean density estimate of 1.66 ± 0.21 tigers/100 km² of this study is strikingly similar to both of these estimates.

**Extinction Risk of Taman Negara Tigers**

The demographic and social structure of rainforest tiger populations is poorly known. Based on demographic data of typical tiger populations in India and Nepal, the estimated 68 adult tigers in Taman Negara would consist of at least 24 breeding females (Karanth and Stith 1999). According to the simulation model predicting extinction probabilities (Karanth and Stith 1999), at the perceived level of poaching of both tigers and prey, the current Taman Negara tiger population appears to be viable at least for the next 100 years (Figure 3-5a). Possible effects of environmental catastrophes, diseases, and genetic deterioration on long-term population viability were not taken into consideration. The model predicts that the extinction risk becomes only significant when the survival rate of cubs is reduced below 50% by prey depletion, suggesting
that a large population is immune to moderate levels of prey depletion. The authors cautioned that
in reality, however, the effects of prey depletion are likely to be much more severe than those
projected by the conservative models because prey depletion is likely to affect survival rates of all
age groups instead of just cubs. Furthermore, the proportional effect of prey depletion on
reduction in tiger population increases as carrying capacity of the breeding females decreases
(Figure 3-5b). Therefore the resilience of the tiger population against the effects of prey depletion
can be sustained only if the carrying capacity is maintained at a high level.

Even a large population, however, is not immune to effects of tiger poaching. The model
predicts that at a small suppression of 10% in survival rates of juvenile to adult tigers due to
poaching can bring the population to extinction in 80-100 years (Figure 3-5a). The insignificant
evidence of poaching found in the study sites and areas covered by the Tiger/Rhino Protection
Units (IRF 2002) cannot rule out the possibility in other parts of this large park with a boundary
of about 426 km. Further investigation is needed in other parts of the park to assess the reality of
the poaching pressure. Strengthening the protection units to patrol longer days and to cover more
areas will definitely enhance the protection level in Taman Negara.

**Tiger-prey Community in Taman Negara**

Although prey selection of tigers could not be determined in this study, potential tiger’s
food habits in a typical rainforest was explored. Concealment and stalking are the main hunting
strategy of tigers (Schaller 1967, Sunquist et al. 1999, Karanth 2001) and prey are located
primarily by sight (Schaller 1967). In the rainforest, where visibility is greatly reduced, the
proportion of prey species taken by tigers may simply reflect the rate of encounter, hence relative
abundance of prey species. It was found that large prey (i.e., sambar and gaur) was extremely
scarce in Taman Negara at 0-0.22 animals/km² (Table 3-5) with occupancy rates as low as 46%
for sambar and 4% for gaur (Table 3-7). In rainforests where prey density is typically low, and its
distribution unaffected by ample availability of water and cover, large predators may be more
opportunistic than selective feeders.
Vertebrate predators in prey-rich habitats are selectively “energy maximizer” (Griffiths 1975). Tigers in Chitwan, for example, showed a preference for sambar (Sunquist 1981); in Kanha tigers selectively killed adult male sambar (Schaller 1967); and in Nagarahole, they selectively killed adult sambar and gaur (Karanth and Sunquist 1995). The nocturnal to crepuscular activity patterns of tigers in these areas reflect the activity patterns of the principal prey. That tigers in Taman Negara were largely diurnal suggests that they were hunting diurnal species such as pig and muntjac, and possibly sun bear. The diurnal tendency suggested by the data was conservative because camera traps were closed during the daytime (0900–1700 h) on the road in Merapoh. Direct observations, captures at night, tracks and feces left on or near the road all suggested that the road was a common access route for tigers in the area.

Wild boar was the most important potential prey species in both abundance and biomass, accounting for 31% to 44% of the total prey biomass. Together with muntjac, these 2 species accounted for 47% to 69% of the total biomass available to tigers (Table 3-5). Furthermore, occupancy rates of these species were 100% in all sites except for wild boar in Merapoh at 88% (Table 3-7). Therefore, I would postulate that the majority of the tiger’s prey consists of pigs and muntjac, 2 of the largest and most locally available prey species, supplemented by whatever else is available as needed.

It may be argued that sun bear is not a typical prey for tigers and the evidence in this study merely suggests opportunistic predation. Sun bear was relatively common, second only to muntjac (Table 3-5) and it was also fairly widely distributed at an average estimated occupancy of 62% (Table 3-7), presenting ample opportunities for predation. Campell (1894), Clutterback (1894), and Lane (1904) reported that tigers killed other bear species larger than sun bears. Clearly not all sun bears are vulnerable to predation, but the same can be said for aggressive male wild boar that can weigh up to 127 kg (Khan 1992). The 3 sun bears killed by tigers were adult animals although dentition suggested that 1 was very old. Because of the abundance and
distribution of this species in the habitat with few large ungulates, I suggest sun bear should be included as a potential prey for this opportunistic predator in the study sites.

Although a fecal sample from Merapoh provided evidence of a tiger killing livestock, livestock was not included in the biomass estimate because I believe that it does not constitute a primary prey for tigers in Taman Negara for the following reasons. First, the hair in the tiger fecal sample was that of a calf and there are no other records indicating that tigers prey on livestock outside the park. Secondly, the fecal sample was collected on the road in Merapoh, which extended to an adjacent oil palm plantation where free-roaming cattle were available. The road provides tigers with easy access to the artificial prey outside the park, and there is no other site with such access. In fact, herds of roaming cattle were observed frequently on the road, only a few hundred meters from where tigers were camera trapped or tracks were recorded. However, during the 19 months spent at Merapoh, I never observed or heard of a case of depredation either from park staff, villagers, or local police. The fecal sample was collected after we moved onto the next sampling site. Thirdly, there are no livestock in areas immediately outside the KT and KK study sites. For the park as a whole, less than 10% of the park’s boundary is adjacent to agricultural lands where livestock occur (Department of Agriculture 1992). And finally, there is limited grazing opportunity in the primary rainforest and the wide rivers that form part of the park boundary effectively keep livestock outside the park. These domestic animals are, in any case, likely to be killed at night by tigers at the edge of the park where the primary forest meets oil-palm plantation. Such cases, if any, are less likely to be reported to authorities because the location of the kill would indicate that the animal was not in a night stall when it needed to be. This makes it exceptionally difficult to assess the extent of livestock depredation. Nonetheless, it is likely that Taman Negara tigers occasionally supplement their diet with livestock outside the park if the opportunity arises.
Tiger Density and Prey Biomass in Rainforests

Animal density is a function of habitat productivity, metabolic needs of the species and size of the area. As such, home range sizes of breeding females are strongly correlated with large ungulate prey (Sunquist 1981). There is a clear relation between prey biomass and tiger density across the tiger’s range (Figure 3-6; $R^2 = 0.78, P < 0.0001$). The estimated tiger densities in the primary rainforest of Malaysia were, as predicted, among the lowest densities recorded in the entire range (Figure 3-6). Based on the average density estimates of large herbivores, excluding elephants, tapirs, and Sumatran rhinoceros (Table 3, O’Brien et al. in press), I calculated the estimated prey biomass of the primary rainforest of Sumatra’s BBSNP to be 408 kg/km$^2$. This was comparable to the biomass estimates at the 3 sites in Taman Negara, which ranged from 266 to 428 kg/km$^2$. There was no difference in the tiger densities between the 2 sites ($X^2 = 0.05, df = 1, P = 0.82$) despite the fact that BBSNP is subjected to heavy poaching of tigers (>8 tigers/year) and prey species (O’Brien et al. in press). Some evidence suggests that tiger poaching rate in GLNP in northern Sumatra is equally high (Griffiths 1994), whereas there were no records suggesting the same for Taman Negara. The high poaching rates in Sumatra may be sustained in a short run by the high recruitment of surviving tigers because both BBSNP (3,568 km$^2$) and GLNP (8,000 km$^2$) are large enough to support more than 40 adult tigers (Griffiths 1994, O’Brien et al. in press).

This study found that based on camera-trapping data, estimation of prey densities was more problematic than estimating tiger density. Line-transect studies conducted in Malaysia in the past could not yield large enough sample sizes within reasonable efforts to estimate ungulate density (pers. comm. Sivanathan Elagupillay, DWNP; Ruth Laidlaw, Wildlife Conservation Society; this study; but see Ickes 2000 for an exception in an area where wild boar was extremely abundant). Until recently there appeared to be only 3 prey biomass estimates for tigers from tropical evergreen forests, all from Indonesia (Hoogerwerf 1970, Seidensticker and Suyono 1980, and Borner 1978 in Seidensticker 1986, Table 5). The crude estimates ranging from 200 to 400
kg/km² led Seidensticker (1986) to conclude that the biomass of essential ungulate prey species for tigers in Asian rainforests do not exceed 500 kg/km². Although the method to estimate the prey biomass in this study was crude and the underlying assumptions untested, the result was as expected of a typical primary rainforest.

Primary rainforests offer little primary productivity at ground level, and thus mammalian biomass is dominated by arboreal herbivores (Eisenberg 1980). Consequently, tropical rainforest is not particularly good habitat for tigers as it does not support a diversity or abundance of large terrestrial ungulates. This study and the studies in Sumatra suggest that a large tract of lowland to hill primary rainforest supports about 1.6 tigers/100 km². This conforms to another report from Sumatra that tiger densities in lowland forests are generally 1-3 tigers/100 km² (Santiapillai and Ramano 1987). The higher end of this generalization applies to more productive lowland rainforest such as of Way Kambas National Park with mixed grassland-forest and secondary forests than primary forest. The tiger density in Way Kambas was found to be 1.6-4.3 tigers/100km² (Franklin et al. 1999).

**Carrying Capacity and Cropping Rate**

There was no evidence for poaching of tigers and their prey in Taman Negara during the study period; thus, the tiger population was probably stable and at equilibrium. Sunquist (1981) estimated that a female and male tiger needed to kill 2629-3286, and 3129-3650 kg of prey/yr for maintenance, respectively. The average weight of adult females and males in his study were 143 kg and 214 kg, respectively. A Bengal subadult female (114 kg; Table 2, Sunquist 1981) appears to be about the size of an average Malay male tiger. As Malay tigers are much smaller than Bengal tigers, the energetic needs for tigers in this study had to be recalculated.

The weight of wild Malay tigers has rarely been measured, but Indochinese and Sumatran tigers are known to be the smallest of the races. Khan (1997) reported average weight of Malay tigers killed in 1970s as 83 kg \((n = 14)\) for females and 92 kg \((n = 15)\) for males. However, these weights were estimated and included juveniles (Blanchard 1977), and thus most likely were
underestimates of adult weights. Two adult male tigers captured at forest fringes in 2000 and 2001 were estimated to be 110 and 130 kg (New Straits Time 2 August 2000, The Star 10 March 2001). The weights of adult Sumatran tigers range from 100 to 140 kg for males, and 75 to 110 kg for females (Mazak 1981). Due to the geographic proximity, and assuming that the size of Malay tigers is similar to that of Sumatran tigers, I used 100 kg for females and 120 kg for males to calculate the energetic needs.

Based on food consumption and weight of large cats (*Panthera tigris, P. leo, P. onca, and Puma concolor*), Emmons (1987) estimated daily food consumption of large cats to be 34-43 g/day/kg. By applying these values to the estimated weights of Malay tigers (i.e., 100 and 120 kg), the estimated annual consumption of female and male tigers is 1241-1570 kg and 1490-1883 kg, respectively. Adding 30% inedible parts of prey to the respective totals, female and male tigers need to kill 1613-2041 kg and 1936-2448 kg of prey annually for maintenance. A tigress feeding 2 large young needs approximately 50% more food (Sunquist et al. 1999). In other words, the weight of prey killed per day is 4.4-5.6 kg for females and 5.3-6.7 kg for males. A tigress with 2 large young needs to kill about 7.5 kg prey/day.

The effective sampling areas in the 3 study sites provided large predators with an estimated 110,400 kg to 151,341 kg of potential prey (Table 3-10). Average body weight per prey animal was 36 kg for MP, 28 kg for KT, and 29 kg for KK. Therefore on average, a tiger must make a kill every 5-8 days in MP, 4-6 days in KT, and 4-7 days in KK. A tigress with 2 large young needs to make a kill every 3.7-4.8 days.

Based on the estimated abundance of tigers at each site, and assuming a male to female sex ratio of 1:3, which appears typical of tiger populations, the estimated cropping rates by tigers ranged from 7.0% to 11.7% (Table 3-10). Including other large predators (i.e., leopard and dhole), the actual cropping rate must be higher. However, leopards may be taking smaller species and a more diverse prey base (Seidensticker 1976, Sunquist 1981, Bothma and LeRiche 1986, Rabinowitz 1989; see Sunquist and Sunquist 1989 for review), which were not included in the
estimated prey biomass for tigers. These may include arboreal/scansorial species (e.g., primates, giant squirrels, civets, and mongooses) and smaller species (e.g., pangolins, moonrats, bamboo rats, birds and lizards). Also because dhole was rare in the park (CPU: 0.04–0.10), the prey biomass collectively removed by all the large predators is probably higher than estimated for tigers alone, but the overall cropping rate may not be too different from estimated.

The cropping rates from Taman Negara are comparable to those reported for large predators in Chitwan (Sunquist 1981), Peru (Emmons 1987), and in East Africa (Schaller 1972). In Chitwan, the estimated cropping rates of tigers were 8-10%, but Sunquist (1981) believed that they were overestimated because livestock was not included in the biomass estimate. The addition of livestock would, however, compensate for losses to leopards and the cropping rate of 8-10% probably approximates the overall offtake by tigers and leopards. In Manu, Peru, jaguar and puma removed a minimum of 8% of the standing-crop biomass (Emmons 1987). In Serengeti, the largest predator, lions, removed 4.6-5.5% of estimated prey biomass and all the large predators collectively removed 9-10% (Schaller 1972). The result of this study conformed to the limiting predator-prey equilibrium state of approximately 10% annual cropping rate (Emmons 1987). The above calculations assume that 30% of the prey biomass is non edible and the rest of 70% is consumed completely. A higher cropping would result if predators do not consume the carcass completely. In Nagarahole India, for example, where low utilization rates for adult gaur by tigers were observed, Karanth (1993) estimated that 14% of prey biomass was removed collectively by tigers, leopards and dhole. Tigers alone cropped 7.5% of prey biomass (Karanth 1993).

Similarly, the predator-prey ratio in Taman Negara is in line with the results of earlier studies. Sunquist (1981) estimated that Chitwan supported 390-630 kg of prey to 1 kg of tiger, assuming that the average live weight of tigers was 111 kg (3/4 of average weight of adult females, Schaller 1972: 454). Using the same assumption, the average live weight of Malay tigers is 75kg, which is equivalent to 68% of the Chitwan tigers. Simply multiplying the ratio of Chitwan by 68%, one would expect Taman Negara to support 265-428 kg of prey/kg tiger. The
actual ratios based on the estimated abundance of tigers and prey biomass at the 3 study sites are 245-321 kg prey/kg tiger. These are similar to large prey: large predator ratios of 249 kg prey/kg predator in Nagarahole, India (Karanth 1993), 250 kg prey/kg predator in Serengeti, Africa or 94-301 kg prey/kg predator in 5 African savanna ecosystems (Schaller 1972). Emmons (1987) reported a ratio of only 135 kg prey/kg large cat in Peru, but the large cats in her study area were less than half the size of Malay tigers; a female puma, and a female and a male jaguar weighed 29, 31 and 37 kg, respectively. A smaller body size of predator reduces the standing crop ratio (e.g., 12kg prey/kg ocelot weighing 8kg, Emmons 1987).

Because predator density is not only a function of standing biomass, but also of turnover rates of the prey species, the high fecundity of wild boar is probably the main factor that allows the predation by large carnivores to be sustainable in the forest with the paucity of large ungulates. In Royal Bardia National Park, Nepal, tigers annually removed 8.5% of wild boar population alone (Stoen and Wegge 1996). The boar density of 4.4 animals/km$^2$ is similar to that of Taman Negara (Table 3-5), and despite the fact that there were larger and more abundant ungulate species available, tigers killed more wild boar than expected (Stoen and Wegge 1996). The highest estimated cropping rates of 9.2-11.7% in this study were coincidentally from the study site with the highest estimated density of wild boar (Table 3-5). After a relatively short gestation of 3.5 months a sow can produce her first litter of 1-8 young at the age of 6-8 months (Diong 1973). With a gestation period of 4 months, the minimum birth interval is usually 7-8 months. In Malaysia, an average number of young produced per breeding sow per year is 5.5 (Diong 1973). The birth interval could be shorter, hence increase in the reproductive rate, if young are weaned early provided that the food source is adequate, or a sow suckles only a few young. In rainforests of Hawaii without natural large predators, a feral pig population is capable of doubling in 4 months (Katahira et al. 1993). In a small isolated forest block in Malaysia without tigers, Ickes (2001) found that the wild boar attained an unusually high density of 47 pigs/km$^2$. He estimated the biomass of wild boar alone to be 1,837 kg/km$^2$. There are no other
reliable pig density estimates from a Malaysian forest, but it is commonly acknowledged by plantation managers and owners of vegetable gardens that tigers help to keep the crop damage by wild boars in control. It is also important to remember that wild boar is a protected species in Malaysia, and it is not consumed by the majority of Malaysians who are Muslims. Furthermore, the Batek, the particular tribe of aborigines that resides in Taman Negara, does not consume wild boar due to a superstitious belief. The second most abundant ungulate, muntjac (Table 3-5) on the other hand, is solitary and after 6 months of gestation (Kenneth and Ritchie 1953) a doe produces an average of 1.5 young per year (Eisenberg 1981). Unlike wild boar, muntjac is the most sought after protected game species in Malaysia, and if the chance arises, the Batek would take muntjac.

In a dry tropical forest of western Thailand, where wild boar occurs in low density due to poaching (Srikosamatara 1993), muntjac was the main prey species for both tiger and leopard (Rabinowitz 1989). The area still supported sambar deer, gaur, and banteng, but tigers rarely killed these largest ungulates either because they were rare and/or not vulnerable. Estimated biomass of large ungulates exclusive of elephants was 1284 kg/km$^2$ (Srikosamatara 1993). If both Bos spp. were excluded from tigers’ prey, the area supported 474 kg/km$^2$ of ungulate prey biomass, which is slightly higher than Taman Negara. Yet, the estimated tiger density of 1 tiger/100km$^2$ (Rabinowitz 1989) would yield estimated cropping rates of 5.1-6.5%, assuming that the weight of average tigers is 150 kg. These cropping rates are probably overestimated. Since some young banteng and gaur might be taken by tigers occasionally, if both Bos spp. were included as prey, the estimated cropping rates decline to 1.9-2.4%. These rates are clearly lower than expected. The scarcity of large ungulates was suggested as 1 of the main factors limiting the tiger density (Rabinowitz 1989), but it is also likely that the most abundant ungulate species year-round in the area, muntjac, simply cannot take the heavy offtake by both tigers and leopards due to its limited reproductive potential (Sunquist et al. 1999).

If tapir were included as prey, the estimated cropping rates in Taman Negara would decline to 1.8%-3.2%. These rates are considerably lower than expected, suggesting that tapir is
probably not a primary prey for tigers. Tapir are, however, both abundant (Table 3-5) and widely distributed (Table 3-7), suggesting that tigers may be avoiding tapir. The old skeletal remains of a tapir was recovered at a saltlick site in the first study site, but the cause of death was unknown.

**Factors Facilitating Coexistence of Tigers and Leopards in Taman Negara**

Due to the scarcity of large ungulates, tigers in tropical forests are forced to take the smaller and more diverse prey items (Rabinowitz 1989), the niche usually occupied by smaller, socially subordinate leopards in more productive habitats (Seidensticker 1976, Sunquist 1981, Karanth and Sunquist 1995). One would then expect high competition between the 2 large felids in Taman Negara. With the underlying principle of competitive exclusion (Gause 1934), resource partitioning and habitat selection are the key mechanisms for species of similar niche to coexist. Karanth and Sunquist (1995), based on data from Nagarahole, postulated that the coexistence of an assemblage of large carnivores species largely depends on relative densities of the different size classes of potential prey, which was also supported by data from Pench and Kanha (Karanth and Nichols 1998). Seidensticker (1976) found that in Chitwan, tigers and leopards differ in size of prey killed, types of vegetation used, and in activity periods. Yet this study seems to have failed to document the fine-tuned adaptation for coexistence. Camera-trapping data suggested that both *Panthera* spp. were active not only during the same period, but also in the same area, sometimes even on the same path. In other words, there was a considerable overlap in habitat use spatially and temporally.

In Kanha where ungulates are abundant, Schaller (1967) found that leopards were resident only in areas where tigers were absent. More detailed study revealed that leopards were relatively scarce in Kanha where large prey (>175kg) was reduced; thus, tigers switched to medium-sized prey, compared to other sites where both –sized prey was abundant (Karanth and Nichols 1998). A similar spatial exclusion of leopards by tigers was observed in Bardia National Park in Nepal where tigers switch to medium-sized prey (Stoen and Wegge 1996). But here, the
food was not a limiting factor since tigers removed only about 3% of the prey. Avoidance of
direct expulsion by socially dominant tigers was suggested as a possible cause.

In contrast, relative abundance indices suggested that Merapoh (MP), where tiger density
was highest, also supported the most leopards (Table 3-8). Leopards were sighted twice during
the day and a cub was also observed on a separate occasion. Although the difference was not
significant, leopards in MP also occupied a larger area than tigers (100% vs. 67% occupancy;
Table 3-8). At 2 other study sites, the abundance and proportional occupancy of leopards and
tigers appeared to be comparable (Table 3-7; Table 3-8). What was so different in MP? I propose
that abundance of primates in MP facilitated the resource partitioning by the 2 congeners, and
supported more leopards than other sites. Although definitive density estimates are lacking,
average frequencies of documenting primates by passive observers were a few times a day in MP,
once every 5 days in Kuala Terengan (KT), and every 3 days in Kuala Koh (KK), which
suggested that the primate populations are greatly depleted in the latter 2 sites.

There are at least 3 factors contributing to the disproportionate primate abundance within
the park. First, primates are the preferred source of animal protein by aborigines who hunt with
blowpipes. There are resident populations of aborigines both in KT and KK, with the former area
supporting a larger population, but they were absent from MP. Secondly, the cultivated land
adjacent to the MP study site was a matrix of oil-palm and rubber plantation as well as fruit
orchards that supported an abundance of primates. Partly as a result of this, a growing population
of pig-tailed macaques became a nuisance at the park compound and had to be trapped and
translocated (pers. observation). Such favorable edge was absent from KK and KT sites. Thirdly,
unique to the MP site, a camera-trap photographed a long-tailed macaque, which is usually not a
forest interior species. It was suspected that this individual might be a survivor of the
translocation program conducted by DWNP in 1991. As part of a pest-control program, DWNP
released about 50 long-tailed macaques in MP. Unlike other monkeys, this macaque is active in
lower branches. It is therefore possible that leopards and even tigers took advantage of the sudden increase of the unusual food source.

Seidensticker (1983) demonstrated that intensity of predation on primates by large cats was negatively correlated with ungulate prey biomass. Clearly some primates are not available to tigers, and this may facilitate the resource partitioning between the 2 species. The hypothesis is supported by 3 out of 4 leopard scats containing *Macaca* spp. The hypothesis can be tested in a more intensive study of the food habits with a greater number of fecal samples, but finding scats in the local forest takes great efforts without an aid of dogs.

In KT and KK where both primate density and large prey were reduced, the 2 congers still coexisted at 1:1 ratio (Table 3-8). I suggest 2 additional factors that may facilitate their coexistence in the prey-poor habitats of rainforests. It relates to the competing species living at low densities in the 3-dimensional habitats. Chances of direct interactions between tigers and leopards are probably limited in rainforests where they both occur at low densities. The 3-dimensional habitat structure of rainforests might further allow leopards to avoid the direct expulsion by tigers while still utilizing the same 2-dimensional space. It can be further hypothesized that the melanistic leopards are better concealed from tigers in the dimly lit ground of the rainforest. Melanism is usually a rare phenomenon. Yet, all camera-trapped leopards in this study and other studies in Malaysia (pers. comm. Wan Shahruddin, DWNP; Ruth Laidlaw, Wildlife Conservation Society; Dionysius Sharma and Mohd. Azlan, WWF-Malaysia), amounting to 100s of leopard photos are of melanistic form. This is in agreement with Gloger’s rule stating that species living in warm, humid conditions have darker coats (Gloger 1833 in Ortolani and Caro 1996). Ortolani and Caro (1996) found a significant association between dark fur and tropical forests across carnivores as a whole, but in neither case was the possible adaptive advantage discussed.

Hutchinson (1959) theorized that competition for food might impose a limit on the similarity between trophic apparati of potentially competing species. The paucity of large
ungulates in tropical forests might have been a factor that has reduced the selection pressure for character displacement in size difference between tigers and leopards. Existing ecological separation between these 2 large cats in tropical forests may be found in much finer grain than that in the prime habitats in Nepal (Seidensticker 1976, Sunquist 1981) and India (Schaller 1967, Karanth and Sunquist 1995, Karanth and Nichols 1998).
Table 3-1
Summary of sampling schedule, efforts and camera-trapping data on tigers collected at 3 study sites in Taman Negara, Malaysia, 1999-2001.

<table>
<thead>
<tr>
<th>Study site</th>
<th>Merapoh</th>
<th>Kuala Terengan</th>
<th>Kuala Koh</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>Camera-trapping period</td>
<td>4/99 – 5/00</td>
<td>3/00 – 1/01</td>
<td>10/00 – 8/01</td>
<td>4/99 – 8/01</td>
</tr>
<tr>
<td>Days camera traps were operational</td>
<td>399</td>
<td>319</td>
<td>300</td>
<td>1018</td>
</tr>
<tr>
<td>Total trap-nights</td>
<td>4,336</td>
<td>4,847</td>
<td>4,871</td>
<td>14,054</td>
</tr>
<tr>
<td>No. trap locations</td>
<td>47</td>
<td>43</td>
<td>45</td>
<td>135</td>
</tr>
<tr>
<td>Tiger photo(^a) (% of total)</td>
<td>22 (1.4%)</td>
<td>14 (1.1%)</td>
<td>25 (1.4%)</td>
<td>61 (1.3%)</td>
</tr>
<tr>
<td>Tiger detection(^b)</td>
<td>12</td>
<td>11</td>
<td>15</td>
<td>38</td>
</tr>
<tr>
<td>Tiger capture(^c)</td>
<td>11</td>
<td>9</td>
<td>15</td>
<td>35</td>
</tr>
<tr>
<td>Effective tiger capture(^d)</td>
<td>8</td>
<td>7</td>
<td>12</td>
<td>27</td>
</tr>
<tr>
<td>No. individual tigers captured, (M_{t+1})</td>
<td>5</td>
<td>5</td>
<td>6</td>
<td>16</td>
</tr>
<tr>
<td>No. trap-nights/tiger photo</td>
<td>197</td>
<td>346</td>
<td>195</td>
<td>230</td>
</tr>
<tr>
<td>No. trap-nights/tiger detection</td>
<td>361</td>
<td>441</td>
<td>323</td>
<td>370</td>
</tr>
<tr>
<td>No. trap-nights/tiger capture</td>
<td>394</td>
<td>539</td>
<td>323</td>
<td>402</td>
</tr>
</tbody>
</table>

\(^a\) Number of photographs of tigers excluding duplicates of the same individual taken simultaneously in a dual-camera setup.
\(^b\) Total number of trap nights tigers were detected at each trap location
\(^c\) Total number of trap nights tigers with known identity were detected. The maximum number of capture of an individual tiger per night is one no matter how many times it is detected at other trap locations.
\(^d\) Total number of tiger captures exclusive of those occurred during the same sampling occasion.
Table 3-2
Body weights and average group sizes used to estimate biomass of herbivores and potential prey species for tigers in Taman Negara, Malaysia.

<table>
<thead>
<tr>
<th>Species</th>
<th>Body weight (kg)</th>
<th>Group size</th>
</tr>
</thead>
<tbody>
<tr>
<td>Great argus pheasant</td>
<td>3</td>
<td>1.00</td>
</tr>
<tr>
<td>Pig-tailed macaque</td>
<td>6.5(^b)</td>
<td>8.60(^c)</td>
</tr>
<tr>
<td>Common porcupine</td>
<td>8(^a)</td>
<td>1.22(^c)</td>
</tr>
<tr>
<td>Sun bear</td>
<td>56(^b)</td>
<td>1.00(^e)</td>
</tr>
<tr>
<td>Elephant</td>
<td>2088(^c)</td>
<td>3.59(^c)</td>
</tr>
<tr>
<td>Tapir</td>
<td>395(^d)</td>
<td>1.00(^f)</td>
</tr>
<tr>
<td>Wild boar</td>
<td>32(^c)</td>
<td>2.23(^c)</td>
</tr>
<tr>
<td>Mouse deer</td>
<td>3(^{ab})</td>
<td>1.00(^e)</td>
</tr>
<tr>
<td>Sambar deer</td>
<td>134(^c)</td>
<td>1.70(^c)</td>
</tr>
<tr>
<td>Muntjac</td>
<td>21(^c)</td>
<td>1.15(^c)</td>
</tr>
<tr>
<td>Gaur</td>
<td>450(^c)</td>
<td>6.99(^c)</td>
</tr>
<tr>
<td>Serow</td>
<td>120(^a)</td>
<td>1.00(^f)</td>
</tr>
</tbody>
</table>

Data source: \(^a\) Medway (1978), \(^b\) Payne et al. (1985), \(^c\) Karanth and Sunquist (1992), \(^d\) Khan (1997), \(^e\) This study, based on average number of individuals photographed at once in the same frame.

Table 3-3

<table>
<thead>
<tr>
<th>Study site</th>
<th>Merapoh</th>
<th>Kuala Terengan</th>
<th>Kuala Koh</th>
</tr>
</thead>
<tbody>
<tr>
<td>No. of Occasion</td>
<td>T</td>
<td>9</td>
<td>9</td>
</tr>
<tr>
<td>Closure test</td>
<td>(P)</td>
<td>0.19</td>
<td>0.94</td>
</tr>
<tr>
<td>Selection criteria</td>
<td>(M_n)</td>
<td>1.00</td>
<td>0.92</td>
</tr>
<tr>
<td></td>
<td>(M_h)</td>
<td>0.86</td>
<td>1.00</td>
</tr>
<tr>
<td>No. of animals captured</td>
<td>(M_{t+1})</td>
<td>5</td>
<td>5</td>
</tr>
<tr>
<td>Estimated average capture probability per sampling occasion</td>
<td>(\hat{p})</td>
<td>0.13</td>
<td>0.16</td>
</tr>
<tr>
<td>Estimated capture probability over all sampling occasion</td>
<td>(M_t + 1 / \hat{N})</td>
<td>0.71</td>
<td>1.00</td>
</tr>
<tr>
<td>Population estimate and standard error</td>
<td>(\hat{N} (SE[\hat{N}]))</td>
<td>7 (1.92)</td>
<td>5 (2.35)</td>
</tr>
<tr>
<td>95% confidence interval of estimate</td>
<td>95% CI</td>
<td>6 to 14</td>
<td>5 to 20</td>
</tr>
<tr>
<td>Coefficient of variation</td>
<td>CV (%)</td>
<td>27.4</td>
<td>47.0</td>
</tr>
</tbody>
</table>
Table 3-4
Mean maximum distance moved by photographically recaptured tigers, effective sampling areas, and estimated tiger density at 3 study sites in Taman Negara, Malaysia, 1999-2001.

<table>
<thead>
<tr>
<th>Study site</th>
<th>Merapoh</th>
<th>Kuala Terengan</th>
<th>Kuala Koh</th>
</tr>
</thead>
<tbody>
<tr>
<td>Area with camera traps (km²)</td>
<td>165.47</td>
<td>164.20</td>
<td>151.41</td>
</tr>
<tr>
<td>Absolute maximum distance moved (km)</td>
<td>6.05</td>
<td>8.22</td>
<td>5.17</td>
</tr>
<tr>
<td>Boundary width (km)</td>
<td>3.03</td>
<td>4.11</td>
<td>2.59</td>
</tr>
<tr>
<td>Effective sampling areas (km²)</td>
<td>353.60</td>
<td>452.50</td>
<td>317.24</td>
</tr>
<tr>
<td>Estimated tiger density and standard error (no./100 km²)</td>
<td>1.98 (0.54)</td>
<td>1.10 (0.52)</td>
<td>1.89 (0.77)</td>
</tr>
<tr>
<td>95% Confidence Interval</td>
<td>1.70 – 3.96</td>
<td>1.10 – 4.42</td>
<td>1.89 – 6.62</td>
</tr>
</tbody>
</table>
Table 3-5

<table>
<thead>
<tr>
<th>Study site</th>
<th>Merapoh Density (kg/km²)</th>
<th>Merapoh Biomass (kg/km²)</th>
<th>Kuala Terengan Density (kg/km²)</th>
<th>Kuala Terengan Biomass (kg/km²)</th>
<th>Kuala Koh Density (kg/km²)</th>
<th>Kuala Koh Biomass (kg/km²)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Great argus pheasant</td>
<td>0.79</td>
<td>2</td>
<td>0.27</td>
<td>1</td>
<td>0.15</td>
<td>0</td>
</tr>
<tr>
<td>Pig-tailed macaque</td>
<td>0.00</td>
<td>0</td>
<td>0.00</td>
<td>0</td>
<td>0.15</td>
<td>1</td>
</tr>
<tr>
<td>Common porcupine</td>
<td>1.46</td>
<td>12</td>
<td>0.33</td>
<td>3</td>
<td>1.02</td>
<td>8</td>
</tr>
<tr>
<td>Sun bear</td>
<td>1.57</td>
<td>88</td>
<td>1.13</td>
<td>63</td>
<td>1.45</td>
<td>81</td>
</tr>
<tr>
<td>Wild boar</td>
<td>4.17</td>
<td>133</td>
<td>3.63</td>
<td>116</td>
<td>4.62</td>
<td>148</td>
</tr>
<tr>
<td>Mouse deer</td>
<td>0.37</td>
<td>1</td>
<td>0.83</td>
<td>2</td>
<td>0.62</td>
<td>2</td>
</tr>
<tr>
<td>Sambar deer</td>
<td>0.20</td>
<td>27</td>
<td>0.01</td>
<td>1</td>
<td>3.22</td>
<td>(0.16)(a) 431 (21)(a)</td>
</tr>
<tr>
<td>Muntjac</td>
<td>3.20</td>
<td>67</td>
<td>3.26</td>
<td>68</td>
<td>4.05</td>
<td>85</td>
</tr>
<tr>
<td>Gaur</td>
<td>0.22</td>
<td>98</td>
<td>0.03</td>
<td>11</td>
<td>0.00</td>
<td>0</td>
</tr>
<tr>
<td>Serow</td>
<td>0.00</td>
<td>0</td>
<td>0.00</td>
<td>0</td>
<td>0.23</td>
<td>28</td>
</tr>
<tr>
<td>Elephant</td>
<td>3.56</td>
<td>7428</td>
<td>0.81</td>
<td>1684</td>
<td>2.10</td>
<td>4382</td>
</tr>
<tr>
<td>Tapir</td>
<td>3.76</td>
<td>1484</td>
<td>1.32</td>
<td>520</td>
<td>2.36</td>
<td>933</td>
</tr>
<tr>
<td>Total</td>
<td>19.30</td>
<td>9339</td>
<td>11.62</td>
<td>2470</td>
<td>16.69</td>
<td>5663</td>
</tr>
<tr>
<td>Total – elephant</td>
<td>15.74</td>
<td>1912</td>
<td>10.81</td>
<td>786</td>
<td>14.59</td>
<td>1281</td>
</tr>
<tr>
<td>Total- elephant –tapir</td>
<td>11.98</td>
<td>428</td>
<td>9.49</td>
<td>266</td>
<td>12.23</td>
<td>348</td>
</tr>
</tbody>
</table>

\(a\) Densities and corresponding biomass of sambar deer and serow in Kuala Koh were clearly overestimated, using the calibration method presented in O’Brien et al. (in press). Adjusted estimates are in parenthesis. The total biomass in Kuala Koh is based on the adjusted biomass. See text for explanation and method used for the adjustment.

Table 3-6

<table>
<thead>
<tr>
<th>Estimates based on (M_o)</th>
<th>Estimates based on (M_h)</th>
</tr>
</thead>
<tbody>
<tr>
<td>(\hat{p}) &amp; (M_{t+1}/\hat{N}) &amp; (\hat{N}(SE[\hat{N}])) &amp; (\hat{p}) &amp; (M_{t+1}/\hat{N}) &amp; (\hat{N}(SE[\hat{N}]))</td>
<td></td>
</tr>
<tr>
<td>Sambar deer</td>
<td>0.16 &amp; 0.93 &amp; 14 (1.21) &amp; 0.14 &amp; 0.87 &amp; 15 (3.18)</td>
</tr>
</tbody>
</table>

\(a\) Selection criteria for \(M_o\) and \(M_h\) models were 1.00 and 0.93, respectively. The closure assumption was not violated \((P = -0.21)\).
Table 3-7
Estimated proportion of area occupied by large mammal species based on monthly surveys of secondary signs and camera-trapping data collected for 5 months each at the 3 study sites in Taman Negara, Malaysia, 1999-2001.

<table>
<thead>
<tr>
<th>Grid size (km²)</th>
<th>Tiger</th>
<th>Leopard</th>
<th>Bear</th>
<th>Muntjac</th>
<th>Pig</th>
<th>Sambar</th>
<th>Deer</th>
<th>Gaur</th>
<th>Elephant</th>
<th>Tapir</th>
</tr>
</thead>
<tbody>
<tr>
<td>Merapoh</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>a</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>$M_{t+1}$</td>
<td>5</td>
<td>7</td>
<td>13</td>
<td>23</td>
<td>19</td>
<td>9</td>
<td>9</td>
<td>9</td>
<td>18</td>
<td>19</td>
</tr>
<tr>
<td>Model used</td>
<td>$M_h$</td>
<td>$M_h$</td>
<td>$M_h$</td>
<td>$M_b$</td>
<td>$M_h$</td>
<td>$M_h$</td>
<td>$M_h$</td>
<td>$M_h$</td>
<td>$M_b$</td>
<td></td>
</tr>
<tr>
<td>$\hat{r}(SE[\hat{r}])$</td>
<td>1.24 (1.76)</td>
<td>(3.2) (3.9)</td>
<td>(3.0) (7.7)</td>
<td>(2.5) (5.0)</td>
<td>(0.1)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>$\hat{\psi}(\text{var}[\hat{\psi}])$</td>
<td>0.67 (0.044)</td>
<td>0.68 (0.025)</td>
<td>1.00 (0.019)</td>
<td>0.64 (0.104)</td>
<td>0.40* (0.041)</td>
<td>0.96 (0.007)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Kuala Terengan</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>$M_{t+1}$</td>
<td>6</td>
<td>5</td>
<td>12</td>
<td>24</td>
<td>24</td>
<td>10</td>
<td>6</td>
<td>13</td>
<td>16</td>
<td></td>
</tr>
<tr>
<td>Model used</td>
<td>$M_h$</td>
<td>$M_h$</td>
<td>$M_b$</td>
<td>$M_h$</td>
<td>$M_h$</td>
<td>$M_h$</td>
<td>$M_h$</td>
<td>$M_h$</td>
<td>$M_h$</td>
<td></td>
</tr>
<tr>
<td>$\hat{r}(SE[\hat{r}])$</td>
<td>1.24 (3.01)</td>
<td>(0.1) (1.4)</td>
<td>(2.6) (2.5)</td>
<td>(5.0) (0.5)</td>
<td>(2.1)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>$\hat{\psi}(\text{var}[\hat{\psi}])$</td>
<td>0.78 (0.038)</td>
<td>0.50 (0.013)</td>
<td>1.00 (0.004)</td>
<td>1.00 (0.011)</td>
<td>0.46* (0.0054)</td>
<td>0.58* (0.011)</td>
<td>0.54* (0.007)</td>
<td>0.71*</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Kuala Koh</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>$M_{t+1}$</td>
<td>7</td>
<td>6</td>
<td>16</td>
<td>26</td>
<td>26</td>
<td>17</td>
<td>1</td>
<td>16</td>
<td>22</td>
<td></td>
</tr>
<tr>
<td>Model used</td>
<td>$M_h$</td>
<td>$M_h$</td>
<td>$M_h$</td>
<td>$M_h$</td>
<td>$M_h$</td>
<td>$M_h$</td>
<td>na^d</td>
<td>$M_h$</td>
<td>$M_h$</td>
<td></td>
</tr>
<tr>
<td>$\hat{r}(SE[\hat{r}])$</td>
<td>2.3 (5.5)</td>
<td>(3.0) (2.7)</td>
<td>(3.1) (4.0)</td>
<td>na</td>
<td>19</td>
<td>26</td>
<td>na</td>
<td></td>
<td>na</td>
<td></td>
</tr>
<tr>
<td>$\hat{\psi}(\text{var}[\hat{\psi}])$</td>
<td>0.78 (0.083)</td>
<td>0.69 (0.371)</td>
<td>1.00 (0.022)</td>
<td>1.00 (0.011)</td>
<td>0.81 (0.014)</td>
<td>0.04 (0.0029)</td>
<td>0.73 (0.0021)</td>
<td>1.00</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

^a$M_{t+1}$ Number of grid cells at which any given species was photographed or detected by signs.

^b$\hat{r}(SE[\hat{r}])$ Estimated number of grid cells at which signs of any given species were present and standard error of the estimate.

^c$\hat{\psi}(\text{var}[\hat{\psi}])$ Estimated proportion of the area occupied by any given species and variance of the estimate.

^dna Presence of gaur was documented only once in one grid, thus no model was available to estimate the site occupancy. The point estimate without variance was based on 1 out of 26 grids containing gaur signs, thus 0.038.

* Ungulate species with proportion of occupancy significantly lower at $P<0.05$ than 100% occupancy of muntjac in the area.
Table 3-8
Relative abundance index (CPU = No. ‘detections’/100 trap nights) of leopards and tigers at 3 study sites in Taman Negara, Malaysia, 1999-2001. Estimated tiger densities are also included for comparison. A ‘detection’ is 1 or more photographs of the species taken at each trap location within a 24-hour period.

<table>
<thead>
<tr>
<th>Study site</th>
<th>Merapoh</th>
<th>Kuala Terengan</th>
<th>Kuala Koh</th>
</tr>
</thead>
<tbody>
<tr>
<td>Leopard CPU</td>
<td>2.40</td>
<td>0.37</td>
<td>0.25</td>
</tr>
<tr>
<td>Tiger CPU</td>
<td>0.28</td>
<td>0.29</td>
<td>0.35</td>
</tr>
<tr>
<td>Estimated Tiger Density (/100 km²)</td>
<td>1.98</td>
<td>1.10</td>
<td>1.89</td>
</tr>
</tbody>
</table>

Table 3-9
Changes in population estimations of tigers at reduced sampling efforts of 56% (5 trapping occasions) and 78% (7 occasions), compared to the original 9 occasions at 3 study sites in Taman Negara, Malaysia, 1999-2001.

<table>
<thead>
<tr>
<th>Study site</th>
<th>Merapoh</th>
<th>Kuala Terengan</th>
<th>Kuala Koh</th>
</tr>
</thead>
<tbody>
<tr>
<td>Sampling efforts (%)</td>
<td>56</td>
<td>78</td>
<td>100</td>
</tr>
<tr>
<td>No. of animal captured</td>
<td>4</td>
<td>4</td>
<td>5</td>
</tr>
<tr>
<td>Estimates based on model M₀</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Capture probability</td>
<td>0.15</td>
<td>0.10</td>
<td>0.15</td>
</tr>
<tr>
<td>Population estimate (SE)</td>
<td>7</td>
<td>4.26</td>
<td>(7)</td>
</tr>
<tr>
<td>Estimates based on model M₂</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Average capture probability</td>
<td>0.25</td>
<td>0.18</td>
<td>0.13</td>
</tr>
<tr>
<td>Population estimate (SE)</td>
<td>4</td>
<td>2.30</td>
<td>(4)</td>
</tr>
</tbody>
</table>

-- No estimates due to no recaptures or only 1 animal captured.
Table 3-10
Estimated available prey biomass and cropping rate for tigers at 3 study sites in Taman Negara, Malaysia, 1999-2001.

<table>
<thead>
<tr>
<th>Study site</th>
<th>Merapoh</th>
<th>Kuala Terengan</th>
<th>Kuala Koh</th>
</tr>
</thead>
<tbody>
<tr>
<td>No. tiger</td>
<td>7</td>
<td>5</td>
<td>6</td>
</tr>
<tr>
<td>Estimated prey biomass (kg/km²)</td>
<td>428</td>
<td>266</td>
<td>348</td>
</tr>
<tr>
<td>Total prey biomass available (kg/site)</td>
<td>151,341</td>
<td>120,365</td>
<td>110,400</td>
</tr>
<tr>
<td>Prey biomass needed (kg/yr)³</td>
<td>11,856 – 14,999</td>
<td>8,469 – 10,714</td>
<td>10,163 – 12,857</td>
</tr>
<tr>
<td>Cropping rate (%)</td>
<td>7.8 – 9.9</td>
<td>7.0 – 8.9</td>
<td>9.2 - 11.7</td>
</tr>
</tbody>
</table>

³ Assuming the sex ratio of 1:3 for male and female tigers as of a typical tiger population.
Figure 3-1
Fluctuations in daily total trap-nights over the course of sampling at 3 study sites in Taman Negara, Malaysia, 1999-2001.

Figure 3-2
Large proportion of elephant and tapir in the estimated total biomass of large herbivore at 3 study sites in Taman Negara, Malaysia, 1999-2001.

Figure 3-3
Relation between estimated tiger density (line) with error bars showing standard errors and estimated biomass of potential prey (bar) at 3 study sites in Taman Negara, Malaysia, 1999-2001.
Figure 3-4
Activity levels (%) of tigers and leopards (a), and their potential prey species (b)-
crepuscular/diurnal species and (c)- nocturnal species, based on pooled camera-trapping data
Figure 3-5
(a) Trajectories of tiger population size (excluding cubs) for simulations that show the basic population (K=24 breeding females), as well as the effects of different levels of tiger poaching (P1) and prey depletion (P2) on the basic population. (b) Probabilities of extinction for tiger populations at different carrying capacities (K=24 to K=3), affected by different degrees of prey depletion.

Source: Karanth and Stith (1999); reprinted with permission from K. U. Karanth and B. M. Stith, also from Cambridge University Press.
Figure 3-6

The significant relation between prey biomass and adult tiger density across tiger range ($R^2 = 0.78$, $p < 0.0001$). The three empty circles represent the data points from this study. Sikhote-Alin (Russia) and Ujung Kulon (Java) have graphically overlapping points.

CHAPTER 4
EFFECTS OF HUMAN ACTIVITIES ON THE TIGER-PREY COMMUNITY

This chapter examines the potential effects of human activities on the tiger-prey community at the 3 study sites, Merapoh (MP), Kuala Terengan (KT), and Kuala Koh (KK), in Taman Negara National Park. Habitat characteristics such as vegetation and topography were similar in all 3 study sites (see Chapter 2, Table 2-1). Thus the following analysis was based on the assumption that any differences in the diversity, abundance, and activity patterns of the predator-prey community at the 3 study sites were attributable to different levels of human activities while other factors were held constant.

Methods

The 2 major legal human activities in Taman Negara involve tourists and aborigines. Prior to initiating my field work, I first combined the registered number of tourists (Department of Wildlife and National Parks Peninsular Malaysia unpublished data; see Chapter 2) and estimated numbers of resident aborigines (van der Schot 1990) to derive an overall level of human traffic at MP, KT, and KK. The level of human traffic at these 3 sites was judged to be low, high, and medium, respectively (Table 4-1). Indices of human traffic based on camera-trapping and track-count data were then used to verify the a priori judgement of human traffic at the 3 sites; these numbers were subsequently used to assess the potential effects of different human traffic levels on species richness, prey biomass, tiger density, and activity patterns of large mammals.

Poaching was assessed by examining clues or evidence found in the park. The effect of forest edges and land use patterns adjacent to the park boundary were also examined for human
impacts by comparing catch per unit effort (CPU = the number of detections per 100 trap nights) of large mammals species at each trapping location. Detections are the total number of trap nights any given species was detected at each trap location. The edge is defined as part of the boundary of study sites adjacent to land areas with different vegetation type, which in this study is either a secondary forest or agricultural crops.

**Assessment of Human Traffic and Activity Levels**

Level of human traffic was assessed by comparing a relative abundance index based on camera-trapping (CPU) and track-count data (RAI\textsubscript{track count}). Based on appearance, humans in photographs were categorized as aborigines, tourists, illegals, park staff, and unknown. Men who do not appear to be aborigines, tourists, or park staff are categorized as illegals by virtue of their illegal entry into the park regardless of their intention. Tourists were easily differentiated because they were found in groups, appeared only on tourist trails and their attire was completely different from men in other categories. Verification of park staff on photographs was done by the park staff. RAI\textsubscript{track count} was a ratio of the number of 100-m transects on the ground with human tracks divided by the total number of transects surveyed. See Chapter 3 for more detailed methodology on camera-trapping and track-count sampling techniques.

Besides the human traffic recorded by camera traps and track-count surveys, other evidence of human activities was opportunistically recorded whenever encountered. This evidence included: 1) etching on tree bark with a knife, which sometimes contains a message for others; 2) campsites; 3) aloewood/agarwood/sandalwood, or locally called gaharu collection sites; 4) traps or snares; 5) footprints; 6) cut marks on vegetation; and 7) others. Aloewood is the much sought after scented wood (non-timber forest product) found as resins produced in response to a fungal infection in some *Aquilaria* spp.

**Potential Human Impacts**

**Species richness.** Cumulative number of species curves were plotted to show how the number of mammalian species camera trapped at the 3 sampling sites changed as sampling
progressed. Then the difference in species richness among the 3 sites was examined by comparing species undetected with camera traps.

**Tiger density and prey biomass.** The tiger density and prey biomass at the 3 sampling sites were estimated in Chapter 3. The results were compared with the different human activity levels at the 3 sites.

**Activity patterns.** Time imprinted on photographs was used to examine potential association of different levels of human activities and activity patterns of the predators (tiger and leopard) and potential prey species (wild boar, muntjac, mouse deer, sambar deer, tapir, and sun bear) at the 3 study sites. The activity pattern was operationally defined as a proportion of numbers of photographs taken at night (1900 – 0659 h) over all photographs. I tested the hypothesis that activity patterns of the selected large mammal species are different among the 3 study sites with various human traffic levels, using 2x3 contingency table analysis (Zar 1984). I expected that animals would be relatively more nocturnal at a site with higher level of human traffic than a site with lower human traffic. Duplicate photographs of the same species taken within an hour at the same trap location were not counted. Gaur \( n = 6 \) and dhole \( n = 9 \) were not included in the analysis due to the small sample sizes.

**Edge effects.** Spatial distribution of wildlife and humans in relation to the park boundary (edge) and the road in MP was examined using ArcView 3.1 (ESRI, Redlands, California, USA) and correlation analysis based on CPU of species at each trap location. The level of significance for all analysis in this section was \( P < 0.1 \). Data collected on the road in Merapoh were excluded from the analysis because it was a unique manmade feature available only in MP. The possible effect of road on wildlife distribution was examined based on data from the forest trap sites and the distance between the trap sites and the road. Spatial distribution of wildlife in relation to saltlick sites was also analyzed in the same manner. Lastly, CPU was also used to examine the possible avoidance of humans by wildlife and other spatial associations among wildlife species.
Results

Assessment of Human Traffic and Activity Levels

Totals of 119, 291, and 308 100-m ground transects were randomly surveyed for wildlife and human tracks, and the RAI_{track count} for humans was 0.025, 0.148, and 0.117 for MP, KT, and KK, respectively. Likewise, for trap-night totals of 4,338, 4,847, and 4,871, there was 49, 467, and 338 photographs of humans taken at MP, KT, and KK, respectively. This translates to 26, 116, 97 detections, and thus the CPU was 0.6, 2.4, and 2.0 for MP, KT, and KK, respectively. By far, MP had the lowest human traffic level, a large proportion of which consisted of illegal trespassers (Figure 4-1). The index based on camera-trapping and track-count data conform to the initial impression of low, medium, and high human traffic levels at the MP, KK, and KT, respectively. Of a combined total of 854 photographs of humans taken at all study sites, no person was carrying a firearm or animal carcasses.

A survey of sign of human activities was conducted for 12 months in MP and 10 months each in KT and KK. Because the number of records continued to increase over time, the data from MP were normalized for a 10-month period for comparison among the 3 sites. We found no evidence of poaching of large mammals in the study sites. No traps, snares, empty cartridges, or animal remains were found at campsites (n = 63). Recording footprints and cut marks on vegetation was discontinued in KT and KK study sites because they were everywhere. Three main types of human activities were etchings on tree bark, campsites, and aloewood collection sites (Figure 4-2). The highest occurrence of sign of human activities from the 10-month samples was at MP (n = 61) followed by KT (n = 58) and KK (n = 41). The type of material used to construct shelters, presence of food wrappers and medicine containers left at campsites, or letters etched on trees suggested that the majority of evidence belonged to aborigines in KT and KK, and at least half the evidence belonged to Thai nationals in MP. Sign of human activities was most abundant in MP where the human traffic level was the lowest. This suggests that sign may not
reflect the current level of human activities at the study sites since, unlike footprints and images captured on film, such evidence can remain in the forest for years after the actual event.

**Potential Human Impacts**

**Species richness.** Between MP and KT, there appears to be little difference in overall mammalian species richness accumulated over time, except that the curve rose faster in MP (Figure 4-3). KK had a lower cumulative species richness curve than 2 other sites. The result was unexpected because species richness is strongly influenced by sample size and KK had the highest numbers of total trap-nights (KK, 4871; MP, 4336; KT, 4847 trap nights) and total detections (KK, 958; MP, 866; KT, 604 detections of mammalian species). However, those undetected species in KK were small mammals (Order Rodentia; Appendix A) or semi-arboreal viverrids (Appendix A) that were not targeted with camera trapping. Camera traps did not detect gaur in KK, but tracks near a salt lick confirmed its presence albeit at an extremely low density with restricted distribution (Chapter 3). Similarly, tracks of Sumatran rhinos were recorded at all the sites although they were never photographed. Thus it is concluded that the presence of medium to large-sized terrestrial mammals were equally represented in the 3 samples.

**Tiger density and prey biomass.** Estimates of both tiger density and prey biomass were highest in MP, which had the lowest level of human traffic and the highest occurrence of signs of human activities. Estimated tiger densities ($\bar{X} \pm SE$) were 1.98 $\pm$ 0.54, 1.10 $\pm$ 0.52, and 1.89 $\pm$ 0.77 tigers/100 km$^2$ at MP, KT and KK, respectively, and the corresponding prey biomass figures were 428, 266, and 348 kg/km$^2$ (Table 3-4, 3-5; Chapter 3). The difference among the tiger densities, however, was not significant ($X^2 = 1.56$, df = 2, $P = 0.46$, Chapter 3). The proportion of ground transects containing no tracks of wildlife were 0.8%, 15.8%, and 6.5% in MP, KT, and KK, respectively, which corresponded well with the estimated prey biomass.

**Activity patterns.** Both large predators and all prey species except for sambar deer and tapir had higher % nocturnality in MP with the lowest human traffic level than other 2 sites, which was opposite of the a priori expectation (Table 4-2). The null hypothesis of equal activity
pattern across the 3 study sites was rejected for leopard ($X^2 = 6.31, P < 0.05$), wild boar ($X^2 = 14.5, P < 0.001$), mouse deer ($X^2 = 3.35, P < 0.05$), sun bear ($X^2 = 5.12, P < 0.10$), and tapir ($X^2 = 6.54, P < 0.05$). These species were all relatively more nocturnal in MP than expected frequencies based on the pooled data from all the sites. Humans were generally diurnal (91%, $n = 294$).

**Edge effects.** In both absolute and relative terms, MP had the longest edge, which accounted for 44% of the study-site boundary (Table 4-3). A boundary adjacent to agricultural lands was considered a hard edge. The proportion of hard edge to the study site boundary was 29%, 5%, and 11% in MP, KT, and KK, respectively. It was therefore expected that edge effects were strongest in MP.

Humans were camera trapped more frequently at locations closer to the park boundary than interior forest at all study sites (MP: $r = -0.26, P = 0.09$; KT: $r = -0.28, P = 0.07$; KK: $r = -0.35, P = 0.01$). Besides humans, wild boar in MP ($r = -0.39, P = 0.01$) responded positively to edges while muntjac ($r = 0.26, P = 0.07$) and elephant ($r = 0.40, P = 0.004$) showed negative responses to the edge in KK. No edge response was observed among large mammals in KT with 5% hard edge. No species except for muntjac in KT ($r = -0.29, P = 0.06$) showed any association to human CPU.

Human CPU showed no correlation with distance to the road in MP ($r = -0.19, P = 0.23$). Leopard ($r = -0.28, P = 0.08$) and sambar deer ($r = -0.27, P = 0.09$) showed positive associations with the road, and tapir ($r = 0.45, P = 0.003$) and gaur ($r = 0.26, P = 0.09$) showed negative association to the road.

Human CPU showed no correlation with the distance to salt lick sites (MP: $r = -0.04, P = 0.77$; KT: $r = -0.26, P = 0.10$; KK: $r = -0.14, P = 0.32$). A strong correlation between CPU and distance to the nearest salt lick was observed for tapir (MP: $r = -0.42, P = 0.04$; KT: $r = -0.28, P = 0.06$; KK: $r = -0.45, P = 0.001$), sambar deer (MP: $r = -0.34, P = 0.03$; KK: $r = -0.42, P = 0.002$), elephant (MP: $r = -0.32, P = 0.04$), and sun bear (KT: $r = -0.32, P = 0.03$). Lastly, tiger CPU showed a strong positive correlation with CPUs of wild boar (KK: $r = 0.44, P = 0.001$),
gaur (KT: $r = 0.56, P = 0.0001$), elephant (MP: $r = 0.4, P = 0.009$; KT: $r = 0.3, P = 0.05$), and leopard (MP: $r = 0.31, P = 0.05$).

**Discussion**

Studies have shown that the abundance of animals is reduced in hunted areas (Glanz 1991, Bodmer et al. 1994, Carrillo et al. 2000, Robinson and Bennett 2000) and that animals shift to become more nocturnal to avoid humans (Ojasti 1991, Griffiths and van Schaik 1993, Guggisberg 1975). There appears to be a negative correlation between abundance of both tigers and prey and level of human traffic at the 3 study sites, but it could not be concluded in a causative manner because this assessment of the human impacts lacked replications of the treatments and random sampling. As suggested by the analysis of species richness, this trend is yet to reach a point where species are effectively extirpated from an area with high human traffic. The rarest large mammals in Taman Negara were Sumatran rhinoceros and gaur. They were both present, albeit in low densities, at all sampling sites (See Chapter 3 and Appendix A).

I had expected that wildlife at KT would shift their activity patterns to become more nocturnal to avoid the high human traffic, whereas the wildlife at MP with the lowest human traffic would show the least % nocturnality. The result showed the opposite pattern. Many species in MP were relatively more nocturnal than 2 other sites. Perhaps the wildlife at MP was responding not to the quantity of the human traffic, but to the type of human activity.

A likely explanation for this trend is that the presence of tourists and aborigines in KT and KK is passive to large mammals. No species except for muntjac in KT showed any association with human CPU. Traditional hunting techniques of aborigines in Taman Negara appear to have little impact on large mammals (Chapter 2). Similarly, the activities of tourists are not likely to affect large mammals. Tourism is a fairly recent phenomenon, but the Batek living in the region are believed to be the direct descendants of the pre-historical men known as the Hoabinhians, who migrated to this area from China 3,000 to 10,000 years ago (Nicholas 2000). Thus wildlife may be habituated to the presence of humans so long as they are not hunted.
Furthermore, the thick cover may allow animals to be active during the daytime, when people are also active. The low density of ungulates in KT and KK may not be a result of poaching, but of resource competition with aborigines. Fruits, tubers, and other edible plants are staples for the natives. The competition may reduce the carrying capacity of some ungulate species. In the absence of such competition, ungulate densities would naturally be higher in MP, which, in turn, would support more predators. This hypothesis can be tested by studying dietary overlap between aborigines and large herbivore species and comparing the standing crop of shared resources in areas with and without indigenous populations.

In addition to the absence of the potential competitor in MP, the large proportion of the study site boundary adjacent to the agricultural crops would increase the food supply for wild boar and primates. As a possible consequence, wild boar in MP was the only species besides human more active and/or abundant near edges. Pigs were probably foraging outside the park and taking refuge and breeding in the park. The average distance of pig nests to the edge ($\bar{X} \pm SD$) was $1.4 \pm 1.3$ km ($n = 8$). No pig nest was encountered in KT and KK. Although still largely diurnal, the % nocturnality of pigs was the highest in MP among the 3 sites or higher than expected frequencies based on pooled data from all the sites ($X^2 = 14.5$, $P < 0.001$).

Besides these differences in human activity levels, a characteristic that stood out in MP was the high number of salt licks, which was likely to influence the abundance of wildlife. There were 5 salt licks in MP and 1 each in KT and KK (Table 2-1). Indices for relative abundance of tapirs, sambar deer, and elephants in MP all showed positive correlation to the proximity to salt licks.

Due to the proximity of oil palm plantations to MP, the pig activity was to some extent predictable; yet surprisingly, tiger CPU did not correlate with the pig CPU. Instead, it correlated with CPUs of elephant and leopard. Among the study sites, elephants were most abundant and widespread in MP (Table 3-5, 3-7; Chapter 3). It is suggested that large predators used the trails maintained by elephants for easy movement. The importance of ease of traveling for animals with
large home range cannot be underestimated. In the rainforest with the low density of large ungulates, predators need to cover large area in search of prey. CPUs of the large predators on the road (tiger: 1.0; leopard: 5.4) were much higher than those in the forest (tiger: 0.1; leopard: 1.7). Both tigers and leopards appeared to make maximum use of the only road in the park for that purpose.

Animals shift to become more nocturnal when they are hunted (Ojasti 1991, Guggisberg 1975). In contrast, Thapar (1989) reports that tigers in Ranthambhore became more diurnal with increasing protection, which also increased the prey base. Because the study found no evidence of poaching, the nocturnal tendency of wildlife in MP is unexplainable. Although we did find more signs of human activities in MP, some of which were fresh, the overall human traffic level was the lowest and human CPU had no spatial association with salt lick sites, proximity to which CPU of ungulate species positively correlated. Thus at least some of the signs observed were of past activities. Increased efforts by DWNP on patrolling in and around park in the past decade probably contributed to the reduction in illegal activities. Yet, the large proportion of signs of human activities in MP belonging to Thais is worrying. MP is particularly prone to illegal activities because it is close to the main highway (Figure 2-1), wildlife is still relatively abundant, no competition with aborigines for aloewood, and chances of being seen and reported to the authority by tourists or natives are close to none. Presence of Thais in Malaysia’s forests primarily in search of aloewood has raised some concerns (Abdul Kadir 1998, Wan Shahruddin 1998, Barden et al. 2000, Bernama 2001), and groups of Thais arrested in Taman Negara in 1992 (Wan Shahruddin 1998) and 2001 (IRF 2002) were carrying wire snares.

Taman Negara is not a pristine untouched forest. Albeit low density, it has had human inhabitants dependent on natural resources for daily survival for at least 3000 years. Their extremely low density (0.046 individual/km²), primitive hunting techniques, and the nomadic lifestyle seem to have kept the resource extraction sustainable in the whole of Taman Negara except when products are harvested for a commercial purpose (e.g. ratan is depleted from Kuala
Tahan area according to park rangers and aborigines). Even if certain heavily hunted species such as primates become depleted in a region with a high concentration of natives, luckily the aborigines are not everywhere in Taman Negara. Neither are tourists. Wildlife may become displaced from areas with high tourism activity, such as Kuala Tahan, but the tourism activities are highly concentrated in a few places in the large national park. Efforts to prevent other types of humans from penetrating into the interior of Taman Negara will ensure the resilience of this large park to absorb the negative human impacts exerted on selected boundary areas. Strengthening the DWNP patrol units and liaisons with aborigines and local villagers as informants would benefit wildlife populations, native populations, and ecotourism in Taman Negara National Park.
Table 4-1
Levels of human traffic by number of tourists and aborigines at Merapoh, Kuala Terengan, and Kuala Koh study sites in Taman Negara, Malaysia.

<table>
<thead>
<tr>
<th></th>
<th>Merapoh</th>
<th>Kuala Terengan</th>
<th>Kuala Koh</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Tourists</strong></td>
<td>low</td>
<td>high</td>
<td>low</td>
</tr>
<tr>
<td><strong>Aborigines</strong></td>
<td>none</td>
<td>high</td>
<td>medium</td>
</tr>
<tr>
<td><strong>Overall</strong></td>
<td>low</td>
<td>high</td>
<td>medium</td>
</tr>
</tbody>
</table>

Data source:

a Department of Wildlife and National Parks Peninsular Malaysia, unpublished data.

b van der Schot (1990) and personal observations, this study.

Table 4-2
Proportion of nocturnal activity for predator and prey species occurring at 3 study sites in Taman Negara, Malaysia, 1999-2001. The number of photographs registered at night (1900 – 0659 h) is in parentheses.

<table>
<thead>
<tr>
<th></th>
<th>Merapoh % nocturnal (n)</th>
<th>Kuala Terengan % nocturnal (n)</th>
<th>Kuala Koh % nocturnal (n)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Tiger</td>
<td>50 (6)</td>
<td>15 (2)</td>
<td>28 (5)</td>
</tr>
<tr>
<td>Leopard*</td>
<td>40 (44)</td>
<td>11 (2)</td>
<td>33 (4)</td>
</tr>
<tr>
<td>Wild boar***</td>
<td>18 (20)</td>
<td>6 (5)</td>
<td>6 (12)</td>
</tr>
<tr>
<td>Muntjac</td>
<td>25 (17)</td>
<td>17 (11)</td>
<td>18 (13)</td>
</tr>
<tr>
<td>Sambar deer</td>
<td>73 (8)</td>
<td>100 (6)</td>
<td>81 (132)</td>
</tr>
<tr>
<td>Mouse deer**</td>
<td>65 (17)</td>
<td>34 (11)</td>
<td>36 (13)</td>
</tr>
<tr>
<td>Sun bear*</td>
<td>39 (24)</td>
<td>23 (11)</td>
<td>22 (13)</td>
</tr>
<tr>
<td>Tapir**</td>
<td>90 (203)</td>
<td>92 (47)</td>
<td>81 (81)</td>
</tr>
</tbody>
</table>

* At P < 0.1, the null hypothesis, the activity patterns of the species are the same among the 3 study sites with different human traffic levels, was rejected.

** P < 0.05

*** P < 0.001

Table 4-3
Distance (km) and characteristics of edges of the 3 study sites in Taman Negara, Malaysia, 1999-2001.

<table>
<thead>
<tr>
<th></th>
<th>Merapoh</th>
<th>Kuala Terengan</th>
<th>Kuala Koh</th>
</tr>
</thead>
<tbody>
<tr>
<td>Study site boundary</td>
<td>81.7</td>
<td>69.3</td>
<td>74.2</td>
</tr>
<tr>
<td>Park boundary</td>
<td>36.3</td>
<td>17.0</td>
<td>24.2</td>
</tr>
<tr>
<td>Boundary adjacent agricultural lands</td>
<td>24.0</td>
<td>3.5</td>
<td>8.3</td>
</tr>
<tr>
<td>Boundary adjacent to forests</td>
<td>12.3</td>
<td>13.5</td>
<td>15.9</td>
</tr>
</tbody>
</table>
Figure 4-1
Levels (CPU = catch per unit effort) and types of human traffic based on camera trapping data at the 3 study sites, Merapoh (MP), Kuala Terengan (KT), and Kuala Koh (KK) in Taman Negara, Malaysia, 1999-2001.

Figure 4-2
Three main types (a) of evidence of past human activities encountered at the 3 study sites in Taman Negara, Malaysia, 1999-2001. Based on clues left behind, it was often possible to identify who left the evidence (b).
Figure 4-3
Cumulative number of mammalian species detected with camera traps at the 3 study sites in Taman Negara, Malaysia, 1999-2001.
Estimated tiger density \( \bar{X} \pm S_E \) in Taman Negara National Park, a primary rainforest of Peninsular Malaysia, was \( 1.66 \pm 0.21 \) tigers/100 km\(^2\) \((n = 3)\). This represents the first statistically valid model-based tiger density estimate from a rainforest in Malaysia. The density estimate was, as predicted, among the lowest densities recorded across the tiger’s range. Furthermore, the estimate from Taman Negara was strikingly similar to 2 other estimates from Sumatran primary rainforest at \( 1.65 \) tigers/100 km\(^2\) (Griffiths 1994) and \( 1.56 \) tigers/100 km\(^2\) (O’Brien et al. in press).

The camera-trapping sampling technique in the mark-recapture framework was successful in estimating the tiger density, but the effort required to collect sufficient samples was impractical for most applications. Furthermore, incorporating heterogeneous capture probabilities in the estimation models was the strength of the program CAPTURE, yet the sample sizes were too small to test for the heterogeneity. This study thus reported the results under the most robust model \((M_h)\), which assumes capture probabilities vary among individual animals but remain constant over time. Because it took about 11 months to sample for tigers at each of the 3 study sites, which were nested in a large contiguous forest, the closure assumption might have been violated both geographically and demographically. Because of the small sample sizes, however, the test statistic had little chance of rejecting the closure. The limitations of small sample sizes were, however, inevitable natural consequence of studying secretive low-density animals in rainforest habitat.

The total effective trapping area constituted about 30% of the park’s lowland to hill forest \((< 900 \) m ASL\), which covered 90% of the park. Based on the density estimate, I estimated the
tiger population in the park to be 68 (95% CI: 52-84) adult tigers or 91 (95% CI: 70-112) adults and cubs.

During the 34 months of sampling, we uncovered no evidence of poaching of large mammals in the park. At the perceived minimal level of poaching, the current Taman Negara tiger population appears to be viable for at least 100 years according to a simulation model computing extinction probabilities (Karanth and Stith 1999). However, the resilience of a large tiger population against the effects of prey depletion can be sustained only if the carrying capacity of tigers is maintained at the high level. The model further predicts that at a small suppression of 10% in survival rates of juvenile to adult tigers due to poaching can bring the population to extinction in 80-100 years.

Only 7 out of 44 large fecal samples collected were of tigers or leopards, and thus the prey selection of the large predators could not be determined. Two fecal samples and a kill suggested that the sun bear was a potential prey species of tigers. The sun bear was relatively abundant and wide spread in Taman Negara. I thus assumed primary prey species of tigers in Taman Negara were ungulate species weighing > 2 kg, and sun bears. Asian elephants and Sumatran rhinoceros were excluded as potential prey. Abundance estimation of prey densities was even more problematic than that of tiger because the mark-recapture models based on photographic captures was not applicable and line-transect sampling did not yield enough data. I used photographic data to make a crude inference on available prey biomass by adopting the calibration regressions from a study in Sumatra (O’Brien et al. in press). The estimated total biomass of large herbivores at 3 study sites ranged from 2470 to 9339 kg/km², largely depending on the density estimates of elephants. Two of the mega-herbivore species, elephant and tapir, contributed 93% of the total biomass. Estimates of available prey biomass ranged from 786 to 1912 kg/km² including tapirs, or 266 to 428 kg/km² excluding tapirs. There was a weak positive correlation between estimated tiger density and prey biomass. Although the method to estimate
prey biomass was crude and the underlying assumptions untested, the result was as expected of a typical primary rainforest.

Wild boar was the most important potential prey species in terms of abundance and biomass. Together with muntjac, these 2 species accounted for 47% to 69% of the total biomass available to tigers. Corresponding to the activity pattern of these 2 large ungulates, tigers in Taman Negara were largely diurnal. I thus postulated that the majority of the tiger’s prey consists of wild boar and muntjac, supplemented by whatever else is available as needed. The largest potential prey species, gaur and sambar deer, were extremely scarce in the park at 0-0.22 animals/km² with occupancy rates as low as 46% for sambar and 4% for gaur. Despite their large size, these 2 nocturnal species were unlikely to be the principal prey of tigers in Taman Negara.

Excluding tapir as prey species, whose depredation by tigers is unknown, the study sites provided large predators with an estimated 110,400 kg to 151,341 kg of potential prey. Annual consumption rates of female and male Malay tigers were estimated at 1241-1570 and 1490-1883 kg, respectively. Estimated cropping rates of 7.0%-11.7% in Taman Negara were comparable to those reported for large predators elsewhere. If tapir are included as prey, the estimated cropping rates would decline to 1.8%-3.2%. These are considerably lower than expected, suggesting that tapir, another large and chiefly nocturnal ungulate, is probably not a primary prey of tigers.

There was a considerable spatial and temporal overlap between tigers and leopards at all the study sites. The study seems to have failed to document the fine-tuned ecological separation of the 2 congeneric predators. In Merapoh (MP), with abundant primates, leopards were much more abundant and widespread than tigers. Two possible factors that may facilitate their coexistence in the prey-poor habitats of rainforests were 1) reduced possibility of direct encounters due to the low densities they occur, and 2) the 3-dimensional habitat structure of rainforests that may allow leopards to avoid a direct expulsion by tigers while still utilizing the same 2-dimensional space.
In MP, where elephants were abundant, both tigers and leopards appeared to use the trails maintained by elephants for easy movement. Probably for the same purpose, both predators were camera-trapped more frequently at trap sites on the road than in the forest. Wild boar in MP was the only wildlife species camera-trapped more near forest edges. The large proportion of the MP boundary adjacent to agricultural crops probably increased food supply for the wild boars, which might in turn have increased tiger density.

Three major sources of possible human impacts on the tiger-prey community in Taman Negara are aborigines, tourists, and poachers. A negative correlation between level of human traffic and abundance of large mammals was observed, but overall impacts on the tiger-prey community appear to be minimal in Taman Negara because 1) the study found no evidence of poaching of tigers or prey, 2) primitive hunting techniques of aborigines appear to have little effect on large mammals, 3) the aborigine density in the park is extremely low at 0.046 individuals/km² and their range of activity does not cover the entire park, and 4) areas affected by tourists are limited to small areas near park boundary and on the trails leading to Mt. Tahan.

Contrary to my expectation, wildlife in MP with minimal human traffic level was more nocturnal than expected. Although there was no evidence of poaching, the signs of other illegal human activities were most abundant in MP. The discrepancy between the traffic level and signs of activities could be explained by the majority of the signs being old. Increased effort by DWNP on law enforcement in the past decade probably contributed to the reduction in illegal activities. Presence of Thai nationals in the park is still worrying. Continuous efforts in law enforcement is needed to ensure the resilience of this large park to absorb the negative human impacts exerted by legal activities in selected areas.
CHAPTER 6
IMPLICATIONS FOR MANAGEMENT AND CONSERVATION OF TIGERS

The long-term persistence of tigers in the cultural and environmental landscape of Malaysia is not assured. The most important action for the conservation of tigers in Malaysia is the active protection of wild populations of tigers and prey. Currently, Malay tigers are distributed widely but sparsely throughout the forest reserves and protected areas of the Peninsula. Because a large proportion of the forest coverage in Peninsular Malaysia is forest reserves rather than protected areas, there are more tigers in unprotected areas. In these unprotected areas, however, large carnivores such as tigers and leopards are subject to persecution and official removal as a result of conflicts with humans. The total number of tigers shot, poisoned, or officially removed is unknown. Thus conservation status of tigers in unprotected areas is unknown. Tigers and other wildlife are best protected in Taman Negara National Park due to its vastness, remoteness, legislation, anti-poaching patrols, and passive presence of tourists and aborigines.

This study provided the first density estimate of tigers in Taman Negara. Tiger density and the corresponding prey biomass estimates are in line with figures from other tropical rainforest habitats. The findings suggest that the Taman Negara tiger population is viable for the next 100 years if the poaching level remains low. Such optimistic forecast for tigers cannot be given for other places in Malaysia. In the next 100 years, further habitat fragmentation and loss of the remaining forests will create more human-tiger conflict areas, where tiger will always lose, and thus a series of extirpation of small populations are expected. The conflicts between humans and tigers will not be resolved, but only intensify under the current trend of human population growth, land use patterns and policies, poverty in the rural areas, poor livestock management, and
lack of proactive management strategies. The increasing conflict with humans is a management problem that requires immediate attention, and thus drains limited resources from other conservation initiatives. Consequently, more long-term proactive measures for conservation of tigers have become secondary. I emphasize that the conservation priority must be given to the area with the best prospects. When tigers are gone from Taman Negara they are gone from Malaysia.

This chapter first provides recommendations on application of camera-trapping techniques to monitor tiger populations in rainforests, then discusses implications of the results of this study for management and conservation of tigers in Taman Negara in particular, and Peninsular Malaysia in general. The discussion focuses on priority issues and areas, thus ex-situ conservation programs and intervention strategies for populations at risk (i.e., translocation, assisted reproduction, etc.) are not addressed.

**Recommendations on Application of Camera Trapping in Monitoring Tiger Population in Rainforests**

The large roadless primary rainforest of Taman Negara was probably the most difficult place to sample population of tigers in Malaysia. Due to the intensity of the trapping effort required to collect adequate sample sizes, the technique may be too expensive and time consuming for monitoring of tiger populations in a mark-recapture framework at multiple sites in Taman Negara or other similarly large rainforests. The following suggestions are made to reduce sampling effort without compromising the data, which will improve the feasibility of using the technique in the rainforest ecosystem.

1. Select a type of camera trap that will remain operational for extended periods of time in wet humid conditions (see Appendix B). Unlike the situation in this study (Fig. 3-1), if all cameras were functioning throughout the sampling session, the chance of missing tigers towards the end of every trapping session would be reduced, thus the capture probability is improved. On a few occasions we recorded tiger tracks in front of cameras that were not
functioning for one reason or another. An improvement in camera-trapping efficiency in term of success rate and functionality will yield a comparable number of trap-nights in a shorter period.

2. Invest more time on reconnaissance and interviews prior to selection of camera-trapping sites. An improvement in the knowledge of tiger movements in the study sites will increase the capture probabilities or the same probabilities can be attained in a shorter period. Data from Merapoh show that both tigers and leopards frequently used the only paved road in the park. Thus in areas with park roads or logging roads, with a priori knowledge of tiger movements, sampling efforts could be greatly reduced.

3. Increase the awareness and support of aborigines and local villagers for research activities. After a few cases of vandalism, we had to close a few traps in areas that offered a good chance of capturing tigers. Aborigines were informed and a group of men often worked with us, but some youngsters were still mischievous — not breaking the cameras but exposing the entire roll of film. Alternatively, a better protective casing for camera trap could be designed (see Karanth et al. 2002, Appendix 5.0), but the size and additional weight are likely to impose an additional physical constraint to the field team. Where camera-trap sites are likely to remain permanent and used for long-term monitoring, an investment in heavy-duty protective cases may be a worthwhile investment.

4. Explore a variety of methods to maximize the capture probability of tigers. Use of olfactory lures or baits may be of some interests in future studies.

If intensive monitoring of the tigers in Taman Negara is only feasible at one site, I would recommend Merapoh for the following reasons:

1. The one and only road in the park greatly facilitates the transportation of equipment and the field team. As a result, cameras can be visited for maintenance more frequently than in other sites, which, in turn, improves the capture probability.
2. The study identified the road and paths leading to nearby saltlicks to be hot spots for tiger movements. Such prior knowledge of tiger movement is important to improve the capture probability. Also, sampling of the area can be done with ease using the road. Two additional salt lick sites in the southern end of the sampling area can also be readily reached by boat on the main watercourse.

3. The road also provides the best opportunity in the park for collection of scats and direct observation of animals, including tiger, leopard, and dhole.

Due to the accessibility, proximity to towns, and availability of facilities, more research not only on tiger ecology, but also on variety of subjects can be conducted in Merapoh. Presence of non-invasive researchers in the forests may further deter illegal trespassers.

Recent camera-trapping studies of tigers in other parts of Malaysia have already shown better capture rates (capture per unit effort) than in this study (Carbone et al. 2001, pers. comm. Dionysius Sharma and Mohd. Azlan, WWF-Malaysia). Other forest habitat types such as secondary forests or mosaics of degraded forests and plantation would provide better foraging opportunities for large ungulates, thus possibly supporting higher density of tigers. Whether the higher capture rates reflect higher tiger densities can be assessed using CAPTURE. In such areas where presence of roads facilitate the easy movement of tigers and field crew, and habitat edges enhance prey biomass, camera-trapping technique in the framework of mark-recapture population estimation models is highly recommended for estimation of abundance. Anticipating that even in more productive habitats, tiger densities in tropical evergreen forests are unlikely to attain the same level found in the rich alluvial grassland or moist temperate deciduous forests of India and Nepal (Figure 3-6), I would thus recommend a minimum of 100 km² or so as a sampling area, which would hopefully contain home ranges of 2-4 adult tigers.

Alternatively, camera-trapping data can be used as indices of relative abundance for both tigers and prey species (Karanth and Kumar 2002). However, the strength of the relationship between the index and true abundance remains unknown until the index is validated with an
independent estimate of absolute density (e.g., O’Brien et al. in press). Relative abundance index from count statistics is based on an assumption of equal proportional constants or capture probabilities (Nichols and Karanth 2002b). Thus, if the assumption is untested, investigators must try to reduce differences in capture probabilities. See Nichols and Karanth (2002b) for further discussion on assumptions and uncertainties associated with indices of relative abundance. Furthermore, the use of expensive camera-trapping techniques to derive only a relative abundance index needs to be justified over much cheaper track-count methods that can also provide similar results.

This study made strong untested assumptions to estimate the prey biomass by adopting the calibration of camera-trapping data against line-transect density estimates from a Sumatran rainforest (O’Brien et al. in press). The reliability of the estimation will improve if an intensive line-transect sampling of prey species is conducted in an area in Taman Negara with relatively abundant wildlife such as Merapoh.

If efforts are made to reduce bias, and count statistics are collected from replicated, random samples in a standardized manner, indices can be a useful tool to monitor the trend over time. I recommend an indices-based monitoring be conducted routinely every few years and a abundance-estimation study be conducted every 10-20 years to monitor the Taman Negara tiger population.

Conservation of Tigers in Taman Negara

The highest priority for conservation of tigers in Taman Negara is on-the-ground protection of tigers and the prey species by anti-poaching patrols. The Department of Wildlife and National Parks Peninsular Malaysia (DWNP) currently has 7 Tiger/Rhino Protection Units (TRPU) operating within Taman Negara. Four TRPU units were first activated in 1995 primarily to protect the critically endangered rhino, but the units were later expanded to protect tigers as well. Furthermore, in response to evidence of illegal activities, DWNP has established additional guard posts on main rivers in the late 1990s. This study found no evidence of poaching of large
mammals within areas encompassing about 600 km² between 1998 and 2001, suggesting that the anti-poaching efforts by DWNP were effective. I commend the efforts and commitment to the protected area by DWNP.

An absence of evidence of poaching from the study area, however, does not guarantee the same for the whole of Taman Negara. I must emphasize again that the anti-poaching patrol must be continued and hopefully expanded to areas that are not covered by TRPU. The monthly average of patrol days per unit between 2000 and 2002 has been less than a week (IRF 2002); provided that the funding is available, the patrol days should be increased. A possible threat to tigers in Taman Negara and other protected areas is the illegal activities by people from neighboring Thailand (Abdul Kadir 1998, Wan Shahruddin 1998, Barden et al. 2000, Bernama 2001). Because there was ample evidence of the presence of Thais in the park, and some Thais were found with snares (Wan Shahruddin 1998, IRF 2002), any wildlife species, including tigers and rhinos, may be targeted. A slight reduction in the survivorship of juveniles to adult tigers due to poaching of tigers will increase the extinction risk. The effort to eradicate foreigners who threaten Malaysia’s national heritage and security must be continued. TRPU has been partially funded by international funding agencies. The anti-poaching efforts, which play such a vital role in wildlife conservation, should not depend on the availability of external funding sources. Commitment to the most important tiger conservation activity by the Malaysian Government is essential to raise funds and support for other secondary conservation activities. Thus I highly recommend the operation cost of the expanded TRPU be included in the fiscal budget of DWNP. Alternatively, the core anti-poaching patrol units (the current 7 units) need to be supported fully by the DWNP, and additional funds can be sought to increase the number of units.

Patrol efforts need to be increased at Merapoh. The area is prone to illegal activities due to the proximity to the main road, absence of aborigines, and abundant wildlife. Four saltlick sites are close to the jeep track, the only road in the park, or park boundary where camera traps have been stolen. These areas require intensive patrolling. Although park officials may be concerned
that patrol units may disturb wildlife, displaced wildlife is better than dead ones. Much of Taman Negara can probably be lightly patrolled because of its remoteness, but an area such as Merapoh requires management intervention. Illegal campsites are easily monitored for the extent of use. In any case, all camp sites found by our research teams were demolished, but some were reconstructed by users. I recommend the patrol units monitor the camp sites and frequent travel routes; a map depicting all the locations has already been supplied to DWNP.

Members of TRPU should be well paid so that it can continue to attract high-quality candidates. Aborigines have extensive knowledge of the forest, including locations of illegal activities. Villagers living adjacent to Taman Negara sometimes have important information about illegal activities. The cooperation of these local populations should be considered critical enough to pay them rewards for this information.

TRPU not only patrol the remote forests, but also collect data on rhino and tigers. If such data are incorporated into the DWNP GIS-based Management Information System or at least into a Taman Negara database, they will be of use for the future monitoring and research. Quality control of the data and standardized data collection and management systems will be important.

Taman Negara must remain inviolate. A proposal by DWNP and Ministry of Science Technology and the Environment to nominate Taman Negara as a World Heritage Site is currently under consideration by UNESCO. Such international promotion of Taman Negara for conservation and ecotourism will hopefully deter any local temptations to either develop or log part of Taman Negara, which is highly possibly during an economic recession. The current entrance fee of RM1 (US$ 0.25) needs to be raised to at least RM10 for foreign visitors so that the value of Taman Negara is adequately appreciated and the park yields some revenue, which may justify the Federal Government to invest more in conservation. Intensive ecotourism activities should not be allowed beyond the designated recreational areas. The balance between ecotourism and wilderness is easier to maintained when the ecotourism is concentrated in a small
area and displaced wildlife has large refugee. Findings of this research should be made available
to the public to promote the conservation significance of Taman Negara.

There currently is no active management of tigers or prey species in Taman Negara.
There is nevertheless room for habitat enhancement for ungulate species (e.g., supplementary salt
blocks at salt lick sites, clearing of vegetation to create grazing ground, or girdling of trees to
create small forest openings), all of which could be carried out in an experimental manner.
Protection of existing populations, however, takes precedence over any habitat management.

**Beyond Taman Negara- Greater Taman Negara Landscape**

Taman Negara National Park is set in a larger cultural and environmental landscape. The
long-term viability of Taman Negara’s tiger population needs to be evaluated as part of the large–
scale tiger-prey communities in the surrounding forests. Together, these large clusters of forests
and small agriculture holdings, villages, and man-made structures form the Greater Taman
Negara Landscape (GTNL). The research initiatives for tigers in Taman Negara will continue to
expand into the GTNL. A preliminary examination of recent satellite photos has identified 2
critical areas that are needed to retain landscape linkages within Malaysia’s Northern Forest
Complex (Figure 6-1), which appears slightly contracted from the originally proposed Tiger
Conservation Unit 1 (Dinerstein et al. 1997). The 2 critical areas are located west and north of
Taman Negara but within the GTNL. GTNL is increasingly isolated from the Main Range forests
at Critical Area 1 following the completion of North-South highway in 1990s and subsequent
land development surrounding the road and a railway, running parallel to the road. In 1985,
construction of a dam northeast of Taman Negara created Lake Kenyir, the largest man-made
lake in SE Asia at 369 km$^2$. This consequently narrowed the forest corridor between Taman
Negara and the forest block north of the park at Critical Area 2. The original TCU 1 will soon be
2 separate units, and possibly 3 if the forest block north of Taman Negara becomes isolated at
Critical Area 2. Complete isolation of the Krau Wildlife Reserve, the second largest protected
area in Peninsular Malaysia, from GTNL is evident after 30 years of land conversion of the
intervening forest. This protected area is no longer a priority area for tiger conservation in DWNP’s Tiger Action Plan (DWNP 1995), and recent surveys documented that only a few tigers remain in the 603-km² reserve (Kassim, et al. 1999, Laidlaw et al. in press). The dwindling tiger population in Krau exemplifies the consequences of forest fragmentation and isolation of a small tiger population in an increasingly human-dominated landscape.

Data on locations and sources of tiger mortalities need to be gathered. Even basic tiger information such as presence and absence is not available from most of the GTNL. Future research in the GTNL should focus on metapopulation dynamics, landscape linkages, and identification of immediate threats to the tiger populations. Continuous law enforcement efforts by DWNP in GTNL should be given priority over any other activities.

The Tiger Action Plan for Peninsular Malaysia (DWNP 1995) needs to be updated, but a mere update will not be sufficient. Achievements, shortcomings, constraints, and actions necessary to overcome the constraints need to be assessed and a periodic evaluation has to be incorporated into the updated Action Plan. Since 1997, the knowledge on tiger ecology and conservation in Malaysia has advanced as a result of collaborative research effort by DWNP (inventories in multiple sites and joint research with the following organizations), University of Florida (this study), World Wide Fund for Nature-Malaysia (a study involving tiger-human conflict resolution and better livestock management), and Wildlife Conservation Society (rapid assessments in multiple forest blocks). It is recommended to establish a task force spearheaded by DWNP to evaluate and update the Action Plan as well as coordinate all aspects of tiger conservation in Malaysia.
Figure 6-1
The Northern Forest Complex (shaded), the main and the largest forest block in Peninsular Malaysia, with arrows indicating 2 critical areas to retain the landscape connectivity within NFC. Main Range forests are increasingly isolating from the Greater Taman Negara Landscape (GTNL) at Critical Area 1. Within GTNL, the narrow forest corridor west of Lake Kenyir connects Taman Negara and the forest block in the north at Critical Area 2. Small isolated forests are omitted for clarity.
Source: base map from DWNP/DANCED (2002).
APPENDIX A

SCIENTIFIC NAMES AND RESULTS OF VERTEBRATE SPECIES DETECTED WITH
CAMERA TRAPS ORRecorded DURING MONTHLY TRACK-COUNT SURVEYS IN 3
STUDY SITES, MERAPOH (MP), KUALA TERENGAN (KT), AND KUALA KOH (KK) IN
TAMAN NEGARA NATIONAL PARK, MALAYSIA, 1999-2001

Reptilian/Avian Species

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<th>Photo</th>
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Mammalian Species

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## Mammalian Species

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<td>Large indian civet</td>
<td>Viverra zibetha</td>
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<td>0</td>
<td>4</td>
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<tr>
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<td>0</td>
<td>14</td>
<td>6</td>
<td>25</td>
<td>14</td>
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<td>Leopard</td>
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<td>113</td>
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<td>24</td>
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<td>Clouded leopard</td>
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<td>Elephant</td>
<td>Elephas maximus</td>
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<tr>
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<td>Dicerorhinus sumatrensis</td>
<td>0(^n)</td>
<td>0(^n)</td>
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<tr>
<td>Tapir</td>
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<td>317</td>
<td>42</td>
<td>78</td>
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<tr>
<td>Pig (Wild boar)</td>
<td>Sus scrofa</td>
<td>132</td>
<td>80</td>
<td>117</td>
<td>151</td>
<td>256</td>
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<tr>
<td>Mouse deer</td>
<td>Tragulus spp.(^bd)</td>
<td>28</td>
<td>17</td>
<td>67</td>
<td>30</td>
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<tr>
<td>Sambar deer</td>
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<td>Naemorhedus sumatrensis</td>
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<td>43</td>
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<td>Mammal total</td>
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<td>312</td>
<td>1266</td>
<td>558</td>
<td>1752</td>
<td>781</td>
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<tr>
<td>Total effort(^e)</td>
<td></td>
<td>4336</td>
<td>119</td>
<td>4847</td>
<td>291</td>
<td>4871</td>
<td>308</td>
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</tbody>
</table>

\(^a\) Total number of photographs.

\(^b\) Animals appeared too small on photographs to be identified to the species level.

\(^c\) Total number of 100-m transects on which tracks were observed.

\(^d\) Two species of the mouse deer, *Tragulus napu* and *T. javanicus*, were pooled as they were sometimes indistinguishable on photographs.

\(^e\) Total trap-nights for camera-trapping data and total number of transects sampled for track data.

\(^\#\) Species that was neither camera trapped nor recorded during track-count surveys, but the presence was confirmed in the study site by sighting (#s), vocalization (#v), or tracks recorded outside the track-count surveys (#t).
APPENDIX B
COMPARISON OF TRAILMASTER® AND CAMTRAKKER® REMOTE CAMERA SYSTEMS FOR DETECTING RAINFOREST MAMMALS IN MALAYSIA

Abstract

While camera-trapping is becoming a common technique in wildlife studies, the equipment is expensive, and thus there is a need to provide a comparative evaluation of the performance of different camera-trap systems in various environmental circumstances and with different species. Two remote camera-trap systems, TrailMaster® (TM) and CamTrakker® (CT), were tested in the lowland rainforest of Taman Negara National Park, Malaysia, between May 1999 and August 2001. Two measures of performance were evaluated: the number of consecutive operational trap nights (effectiveness) and the rate of wildlife photographs for all exposures (efficiency). Both systems successfully detected all the terrestrial medium-to-large-sized mammals known to occur in the park except for the Sumatran rhinoceros (Dicerorhinus sumatrensis). CT was superior to TM in both measures of performance. Mean consecutive trap nights ($\bar{X} \pm SD$) per 30 to 35-day trapping session were 14.0 ± 2.3 for TM and 33.0 ± 4.0 for CT. Mean rates of wildlife photos for all exposures for TM and CT were 0.33 ± 0.05 and 0.85 ± 0.12, respectively. To some extent, the performance of TM depended on experience whereas CT performance was intrinsic to the equipment. TM was sensitive to humidity, animals, and insects. Its sensitivity to unknown extrinsic factors, number of components involved in 1 working unit, and rapid power drainage due to high humidity all contributed to the poor performance of TM. Advantages and difficulties of the both systems and important features of camera traps that need to be considered for applications in a rainforest environment are discussed. The findings provide
researchers with guidance for selection of appropriate equipment, planning the allocation of resources, and preparation for in-the-field troubleshooting.

**Introduction**

Remote photography, conventionally referred to as camera trapping, is becoming a common technique to detect secretive and/or low-density mammals for wildlife studies. It is not entirely a new technique (see Gysel and Davis 1956, Pearson 1959, Osterberg 1962, Cowardin and Ashe 1965), but recently has gained popularity due to commercially available systems. The technique has been used to study a wide range of taxa, including birds (Cowie and Hinsley 1988, Challet et al. 1994), reptiles (Sadighi et al. 1995), small mammals (Pearson 1959, Osterberg 1962), ungulates (Jacobson et al. 1997, Koerth et al. 1997), large carnivores (Foster and Hamphrey 1995, Mace et al. 1994, Karanth and Nichols 1998), and assemblages of rainforest mammals (Seydack 1984, Griffiths and van Schaik 1993, Kawanishi 1995, Kawanishi et al. 1999). Cutler and Swann (1999) provide an in-depth review of the technique.

A remote camera system is the least intrusive method to obtain permanent records of occurrence of multiple taxa day and night for an extended period of time. Camera trapping also provides a unique opportunity to collect information on presence of individual animals, demographic parameters, activity level, distribution, minimum home range, and potential effects of human activities on cryptic animals. The disadvantages of the method are relatively high cost of the equipment (purchase and maintenance), technical difficulties associated with the high-tech equipment, and paucity of literature on technique and various types of equipment. Most existing literature on evaluation of equipment deal with only 1 model — TrailMaster infrared system (Kucera and Barrett 1993, 1995; Rice 1995, Hernandez et al. 1997). However, many researchers are now using a passive-infrared base CamTrakker system (Laidlaw and Wan Shahrudin 1998, Lynam et al. 2001, Walston et al. 2001, O’Brien et al. in press). This paper presents the results of series of performance tests of these 2 widely used infrared remote cameras systems in a rainforest research application.
Study Area

Taman Negara National Park (4°10' - 4°56'N, 102°00' - 103°00'E) is located in north-central Peninsular Malaysia. Encompassing 4,343 km², it is not only the largest national park in Malaysia, but is also one of the largest parks in Southeast Asia. Altitudes range from 70 m to 2,191 m ASL at the peak of Mt. Tahan. Malaysia has a tropical climate with wet, hot and humid conditions year-round and little seasonal variation, conditions that severely test electrical equipment. Based on data collected at several weather stations around the park between 1999 and 2001 (Malaysian Meteorological Service, unpublished data) Taman Negara received an annual average of 2,500 mm precipitation. Annual average relative humidity was 86% with little monthly change from 82% minimum to 92% maximum. Temperature also varied little with monthly maximum temperatures of 30 °C to 34 °C and monthly minimum temperatures of 22 °C to 23 °C. The forest type is broadly classified as a tropical evergreen moist forest, which ranges from lowland humid tropical forest to montane oak (Fagaceae) and ericaceous forests (Weber 1972, Whitmore 1984). The road density in the park is 0.023 km/100 km², representing one of the lowest in the world. This road density provides great protection for wildlife but a logistical challenge for wildlife biologists.

Three sampling areas of 200 km² each were selected based on prior knowledge of presence of tigers, the target species for the research, and availability of logistical support (e.g., accessibility, manpower, field station, and river drainages for transportation). The sites were Merapoh (4°41’N/102°35’E), Kuala Terengan (4°26’N/102°27’E) and Kuala Koh (4°52’N/102°27’E). The altitudinal range of the sampling areas was 70m – 900m and the vegetation was lowland to hill Dipterocarp forest.

Methods

Equipment

Both the TrailMaster (TM) active infrared and CamTrakker (CT) passive infrared systems are equipped with 35-mm, weather-resistant, auto-flash, auto-rewind and auto-focus cameras that
imprint date and time of events on negatives. The TM system electrically triggers the camera when a linear infrared beam is broken by an object. A typical TM system consists of 3 components, i.e., transmitter, receiver, and camera, which is connected to the receiver by an electrical wire. We designed a crude, lightweight casing for the camera to protect it from rain, animals, vandals, and fallen objects. The casing was mounted on a tree with a bicycle cable lock.

To identify individual tigers based on stripe patterns, I needed images of both flanks. This was achieved by a trigger system (TM Multi-Camera Trigger II), an electrical hub that connected the receiver and 2 cameras by 3 wires, and the cameras were set up on opposing sides of game trails. This dual-camera arrangement was discontinued after 2 months due to a persistent problem of moisture infiltrating the trigger mechanism. TM system offered sensitivity adjustments on sensor pulse (i.e., how long the beam needs to be broken for the event to be registered: 0.05 – 1.50 seconds) and camera delay (i.e., the time period between successive photographs: 0.1 – 98 min). TM also allows for setting up timer, which activates and deactivates the system up to twice within 24 hours. Up to 1000 events are stored in the receiver that can be downloaded to a TM Data Collector in the field, later to a computer, and managed with a software provided by the manufacturer.

The CT passive infrared system emits a conical IR beam, which detects differential heat and motion compared to the background ambient temperature, and triggers the camera. To capture both flanks of a tiger, 2 CT units were set up on opposing sides of a path. Choices of time delay between successive photographs are 3, 6, or 10 minutes. The operation mode can be selected from day, night, or continuous. The sensor and camera of CT were housed in a weather-resistant, self-contain casing, which was mounted on a tree with the same cable lock used for TM. After several incidences with the film getting stuck inside the cameras due to condensation or humidity, we placed 2 packets of silica gels inside the casing. More detailed information of the 2 systems, including weight, cost, power source, and set-up specifications used in this study are in Table B-1.
**Sampling Design**

The 3 study sites, Merapoh (MP), Kuala Terengan (KT) and Kuala Koh (KK) were sampled between May 1999 and May 2000, March 2000 and January 2001, and October 2000 and August 2001, respectively. The ultimate goal of camera-trapping was to maximize the capture probabilities of tigers, and camera systems were placed at strategic locations beside active game trails with an average camera density of 1 unit every 4-5 km$^2$. There were 39 trapping locations in MP, 43 in KT and 45 in KK. Trapping locations were by default stationary throughout the sampling period, but camera traps were occasionally moved to nearby areas with fresh tiger sign or shifted to a new location if preliminary results revealed poor animal traffic at the particular site. Limited mobility was a major constraint in this study. Except for a 13-km stretch of road at MP, there were no roads in the park and it usually took 6 to 8 weeks of actual field time, sometimes stretching to over 3 months, to “fill” each 200-km$^2$ sampling area with camera traps, and also to concurrently survey new areas and check cameras set earlier. Although boats were used whenever possible, cameras in most remote areas could be reached only on foot; thus, on average we could set and check 1.5 cameras/day. Thereby, each trap location was visited for maintenance and data retrieval only once a month and thus a trapping session usually lasted 30-35 days.

The selection of which camera system to set at a particular trap location was subjective. Because the initial performance test suggested that CT operated for longer with a higher success rate than TM, wherever the likelihood of capturing tigers was high, CT was chosen if available. I chose TM in areas with high human traffic and set the timer to avoid humans finishing a roll of film prematurely. I chose CT in areas with uneven terrain because it required only 1 tree, and the set up configuration (height and angle) was flexible, whereas TM required 2 straight trees facing each other without objects in between and the set up configuration had to be precise. Besides these primary criteria, selection was dictated by the availability of units. As a result, at 45% of all trap locations ($n = 127$), both TM and CT were used for different times at the same trap location.
This might have reduced the sampling bias associated with the subjective selection of the system, and the chance of a poor result at a specific location due to inferior equipment.

All camera traps were tested for functionality and loaded with new film and batteries in the field station prior to going to the field. Upon arrival at a TM trap location, we first conducted a “test shot” to see if the unit was still functioning, inspected the physical appearance of all the components, replaced the old camera with a new one, downloaded the data from receiver, checked the sturdiness of the sensors and realigned if necessary, and resumed the trapping with another test shot. Sensors were changed every 2 months. The distance between transmitter and receiver was usually 5-10 m depending on the width of the game trail and location of suitable trees. Any vegetation that would trigger the sensor or obscure the images was removed. The general checking procedure was the same for CT. CT units were replaced monthly, even though batteries for the sensor would last for at least 2 months. This is because removing film from the camera in the field was often problematic, and CT does not allow the camera to be separated from the casing. For both TM and CT, when we were short of replacements, only film and batteries were changed in the field using the same unit.

**Data Analyses**

All statistical tests were performed using SPSS version 9.0.0 (SPSS, inc. 233 S. Wacker Drive, 11th floor, Chicago, Illinois 60606, USA). Performance of the 2 systems was evaluated by comparing 2 types of attributes: effectiveness and efficiency at 2 scales: overall results and short-term intensive test.

Effectiveness was measured as the number of consecutive trap nights the particular unit was operational between setting and checking procedures (1 trapping session). A trap night was a 24-hour period during which a camera-trap was functional. Ideally, a trapping session starts and ends with test shots (see above). If a camera system prematurely ceased to function and there was no test shot to complete the session, then the date of the last photograph taken was used as the last day of trapping. In cases where no photographs were retrievable (e.g., camera stolen or damaged
by animals, film damaged by water, no exposures because the camera battery died) the trapping session had 0 trap nights.

Efficiency was a measure of success, determined as the rate of wildlife photographs for all exposures, exclusive of test shots. Excluding test shots, exposures were categorized in 2 groups: 1) “wildlife photo” was a photograph containing any images of wildlife, including human, regardless of the identity, and 2) “nil photo” was a photograph with no discernible image.

**Overall performance**

Camera-trapping results from all trap locations of TM and CT were combined at each study site to compare the overall performance of the 2 systems. The gross effectiveness was first examined by comparing types of wildlife species captured on film and the proportion contributed by each of the 2 systems. Mammalian species with more than 10 photographs were included in this comparison. Number of photographs was normalized by total trap nights accumulated by the particular system. If either system contributed more than 75% of the total photographs of the particular species, it was classified as producing positively biased result. Potential reasons for ineffectiveness of either system in camera trapping any medium to large terrestrial mammals known to occur in the study sites were also examined.

The consecutive trap nights in each trapping session and monthly success rates of TM and CT were first compared within each study site. Then results were tallied from all study sites and divided by number of total trapping sessions to obtain a per trapping-session average performance. Potential improvement in performance of both systems was assessed graphically by plotting average consecutive trap nights and monthly success rates over time.

Lastly, reasons for poor performance were explored by examining the number of trapping sessions with 0 trap nights, hence 0 success rate. This “0 functionality” despite a successful test shot at the beginning of the trapping session is a major limitation of the camera-trapping technique. I believe that the causes for the 0 functionality are reflected in overall poor
performance of a system, and thus they deserve further attention and consideration by both researchers and manufacturers.

**Intensive performance test**

The performance of TM and CT systems were tested intensively between January 30 and May 6, 2000, in Merapoh. At this time, TM units had already been used in the field for 10 months and all CT units were new. A pair of TM and CT units were mounted on the same tree about the same height, focusing on the same area (Figure B-1) at 8 locations chosen randomly out of 39 trap locations in MP. The camera traps were first checked after 1 month during the usual maintenance visits. Because CT was known to operate for more than a month, the test was then extended for another 2.5 months without maintenance. Thus the 2 systems were tested at each trap location for 2 sessions.

The consecutive trap nights and success rates of TM and CT were compared. Causes for 0 trap nights or low success rates were scrutinized on a case-by-case basis. Examination of frequent cases would prepare researchers for trouble-shooting in the field. Potential bias in detecting certain species was assessed by comparing number and type of wildlife photographs missed by either unit at the same location.

**Results**

**Overall Performance**

The TM and CT remote camera systems detected 4 invertebrate and 54 vertebrate species or taxa from May 1999 to August 2001. Among vertebrate species, there were 2 reptilian, 12 avian and 40 mammalian species recorded. TM was responsible for all invertebrate \((n = 66)\) and 86% of all reptilian photographs \((n = 14)\). Among medium to large terrestrial mammals, the only species known to occur in the study sites, but never detected by either camera system was the critically endangered Sumatran rhinoceros (*Dicerorhinus sumatrensis*). A few observations of tracks and feces of rhino were made in all study sites, but they were rare and highly localized. As
soon as researchers investigated and set up a camera trap, the animals seemed to move out and no subsequent sign was again found in the same area.

To assess for potential sampling bias of either system in detecting terrestrial rainforest mammals, numbers of photographs of species with more than 10 records were normalized with the number of total trap nights (i.e., 3,879 for TM and 5,839 for CT), and the proportion of photos taken with each system were compared (Figure B-2). Data from Merapoh (MP) were excluded from this analysis because CT was used only towards the end of sampling; as such the CT trapping session \( n = 30 \) was considerably lower than that of TM \( n = 207 \). In Kuala Terengan (KT) and Kuala Koh (KK), both TM and CT were used throughout all sampling sessions. Both TM and CT were used during different trapping session at 45% of the total trap locations \( n = 88 \). Of 19 species included in this analysis, 16 species were detected no more that 75% by either system; thus, both systems were equally effective in detecting these mammals. Because TM infrared beam was set 50 cm above ground, I expected TM to miss smaller animals. This was indeed the case as brush-trailed porcupines \((Atherurus macrourus, n = 17)\) and mouse deer \((Tragulus spp., n = 103)\) were detected almost exclusively with CT \( n = 118, 98\%\). Data not included in the graph \( n \leq 10\) per species also indicated that CT detected more species of the order Rodentia. All records of serow \((Naemorhedus sumatrensis, n = 51)\) were made with CT because only CT was suitable for use in hilly habitat.

Despite the fact that the total trapping session of CT \( n = 218 \) was less than half that of TM \( n = 460 \), overall CT achieved higher number of trap nights \( n = 6,958 \) than TM \( n = 6,299 \) because on average CT lasted longer in the field. The total exposures with TM was 7,400, 3 times that of CT, but 60% \( n = 4,447 \) and 32% \( n = 2,389 \) of all TM exposures were nil photos and wildlife photos, respectively. Of 2,529 exposures with CT, 16% \( n = 415 \) and 80% \( n = 2,022 \) were nil photos and wildlife photos, respectively. Thus CT was more effective and efficient in camera trapping wildlife. The photographs not categorized as either nil or wildlife were of rain or vehicles. Rain photos comprised 7% \( n = 517 \) of TM and 0.6% \( n = 16 \) of CT total exposures,
and it was uncertain whether the unit was triggered by rain, by wildlife but the image was obscured by rain, or it happened to be raining when the unit produced a nil photo.

The superiority of CT in number of trap nights and success rates in all the study sites (Figure B-3) was substantiated statistically. The Kolmogorov-Smirnov test of normality with Lilliefors significance correlation (Lilliefors 1967) suggested that none of the TM and CT trap-night samples (i.e., consecutive trap nights per trapping session at each trap location) from the 3 study sites came from a normally distributed population. The Mann-Whitney test was used to compare the MP data because the skewness of the TM and CT data was in opposite directions (MPTM = 0.213, MPCT = -1.508) and the sample sizes differ considerably (MPTM = 207, MPCT = 30). The differences in mean trap nights between TM and CT were significant ($U = 755.50$, $Z = -6.763$, $P \leq 0.001$). The t-test is robust to considerable departures from the theoretical assumptions, especially if the skewness is in the same direction (Myers and Well 1991), which was the case with KT and KK data. Welch’s t-test for KT samples with heterogeneous variances ($F = 15.13$, $P \leq 0.001$) suggested that the differences in mean consecutive trap nights between TM and CT were significantly different ($t_{160} = -9.152$, $P \leq 0.001$), while an independent sample t-test for KK samples with homogeneous variances ($F = 0.129$, $P = 0.72$) also suggested that the differences were significant ($t_{231} = -9.150$, $P \leq 0.001$). Monthly success rates of TM and CT at the 3 sites were compared with the Mann-Whitney test. Ranks of the CT success rates in all sites were greater than those of TM (MP: $U = 16$, $P = 0.044$; KT: $U = 49$, $P \leq 0.001$; KK: $U = 60$, $P = 0.021$).

Because the number of units and period of time the 2 systems were used were different, it may be more indicative to assess the performance per trapping session (Figure B-4). In this comparison, CT achieved higher trap nights and success rates than TM. Mean consecutive trap nights ($\bar{X} \pm SD$) for TM and CT were $14.0 \pm 2.3$ and $33.0 \pm 4.0$, respectively. Mean success rates for TM and CT were $0.33 \pm 0.05$ and $0.85 \pm 0.12$, respectively.
Over time TM performance improved, whereas CT performance declined. The per trapping-session average trap nights of TM improved while that of CT declined over time (Figure B-5). Likewise, the monthly success rates of TM gradually improved while that of CT declined over time (Figure B-6).

When data from 3 study sites were pooled, there were a total of 91 and 21 trapping sessions that were registered as “0 trap night” for TM and CT, respectively. The numbers of cases and descriptions of 12 factors determined to be the causes for the 0 functionality are presented in Table B-2. When multiple factors contributed to the 0 functionality and the main cause was unknown, such cases were included in the unknown category. In all factors except for theft and the problem with film-advancing mechanism, TM outnumbered CT in causes for 0 functionality (Figure B-7). Three main causes for the TM 0 functionality were unknown extrinsic variables, malfunctioning equipment and short-life of camera battery. Together, these 3 factors caused 79% of the TM 0 functionality.

**Intensive Performance Test**

Of 8 randomly chosen test locations at MP, 6 locations had 2 trapping sessions, 2 locations had only 1 session, and thus 14 pairs of observations were made. Despite the low total trap nights, TM yielded more exposures, 76% of which contained no images of wildlife (nil). Nil photos comprised only 3% of the total exposures made by CT, which lasted more than 10 times longer than TM (Figure B-8).

The 2 measures of performance were cumulative trap nights and success rates. The mean consecutive trap nights, $\overline{X} \pm SD$ (minimum – maximum) for TM and CT were 3.50 ± 6.94 (0.00 – 20.00) and 46.07 ± 21.28 (24.00 – 72.00), respectively. The mean success rates for TM and CT were 0.14 ± 0.29 (0.00 – 0.97) and 0.95 ± 0.10 (0.70 – 1.00), respectively. The superiority of CT in both measures was further substantiated statistically as follows.

A Shapiro-Wilk test (Shapiro and Wilk 1965) indicated that the differences in consecutive trap nights between TM and CT ($SW_{14} = 0.846, P = 0.02$) and differences in success
rates between TM and CT ($SW_{14} = 0.721, P = 0.01$) did not come from a normally distributed populations. Therefore, Wilcoxon signed ranks tests were performed and the differences in mean consecutive trap nights ($Z = -3.305, P \leq 0.001$) and success rates ($Z = -3.366, P \leq 0.001$) between TM and CT were both significant.

The poor performance of TM was attributed to many observations with the value “0”. Of 14 observations, 9 had 0 trap nights and thus 0 success rate. Determining the exact cause of the TM “0 functionality” is not simple due the number of components involved in 1 working system and its sensitivity to unknown extrinsic variables. Causes for the TM “0 functionality” were similar to the previous assessment of overall performance.

Because there was a high chance of the TM system malfunctioning in the field, a comparison of missed wildlife photographed by either system at the same location was limited to 5 observations. At 3 trap locations, no wildlife photographs were missed by either system, but the consecutive trap nights of TM were all less than 5 nights; therefore, the comparison was made within the 5 nights. At 1 location, TM missed 2 photographs of mouse deer. At another location, TM missed 1 photograph of tapir (*Tapirus indicus*) and CT missed 1 photograph of sun bear (*Helarctos malayanus*).

**Discussion**

The results of both overall performance assessment and intensive test produced overwhelming evidence to suggest the superiority of CT over TM in both effectiveness and efficiency in an extremely wet and humid rainforest environment. The poor performance of TM during the intensive test may be partly due to the fact that the TM units were 10 months old whereas the CT units were new. This was supported by the data, as CT performance gradually declined over time while TM improved over time. TM produced 7,389 wildlife photographs and there was no sampling bias for medium to large terrestrial mammals between the 2 systems. However, I do not agree with Kucera and Barrett’s (1995) argument in response to Rice (1995) that "tropical humidity is not an insurmountable condition,” which was suggested by many photos.
of a tropical species taken with TM by their colleague in Taiwan. To the question “Was TM successful in detecting rainforest mammals?” the answer is “Yes,” as suggested by thousands of wildlife photos. But had it not been for this comparative study of the performance of the 2 systems, “but less efficiently than CT” could not have been added.

The inferior performance of TM might not be so much as a result of an inferior system, but that TM was not suitable for this study. Based on the average trap nights per session, I recommend TM be checked at least every 14 days in tropical environments instead of the suggested once a month for temperate regions (Kucera and Barrett 1993). CT can be checked every 6 weeks given that a roll of film is sufficient for the duration and the CT air-tight casing contains packets of silica gel to prevent the film from sticking in the camera.

As noted by Rice (1995), the problematic feature of TM is the large number of nil photos due to unknown factors. The TM system is comprised of 4 error-free separate components (transmitter, receiver, camera, and wire). One CT requires half the number of components and they are housed together in a weather-resistant protective container. A TM set up with a trigger system and 2 cameras to capture images of both lateral sides of animals would require 8 separate components working in unison. If one goes wrong, the whole system fails and it is not easy to identify the defective components in the field because the film that often provides clues is yet to be processed. Consequently, possibly defective parts are left in the field for another month of poor results. This could be alleviated if all components were changed monthly or more frequently. However, unless the malfunctioning components are identified immediately, they are likely to produce similar results at a different trap location.

Another problem with TM in this application was sensitivity to unexpected extrinsic factors such as fallen branches, animals bumping the sensors, animals chewing the wires, sunlight, rain, flying bats, and insects. Some of these could be alleviated by housing both the sensor and camera in a stronger protective casing such as the one designed and used in India (Karanth et al. 2002). I could not apply their design simply because it was too heavy to carry on our backs.
The metal bracket and mini tripod supplied for the TM camera by the manufacturer were of no use in the presence of playful elephants, bears, primates, ungulates brushing their bodies against trees, people, and falling branches.

Swinging vegetation, mentioned as a major factor causing “false events” by Kucera and Barrett (1995), was not a problem in this study because we took extra care to remove any vegetation between the sensors. This was necessary because fast-growing palm species can grow up to a foot in a month. We avoided direct sunlight hitting the receiver window by facing the receiver to north whenever this was suspected, but generally the forest floor was shaded by thick canopy.

All 8 records of bats were produced by TM. Some of the numerous nil photos taken at night could have been triggered by flying bats. Our selection of the sensor sensitivity was 0.20 seconds, only 0.05 seconds faster than recommended for most applications (TrailMaster Instruction Booklet for TM1000/TM1500, Goodson and Associates, Inc). Since the sensitivity of 0.05 seconds is recommended for detecting flying birds, our setting is not likely the only reason for hundreds of nil photo at night. Activities of insects, reptiles, and small mammals on the tree surface near the ground are sometimes inevitable even though we carefully selected trees with minimal insect activities. In many cases we found ants and termites making nests and laying eggs inside the TM receivers and transmitters, which always caused the units to malfunction. This claim was first made by Rice (1995) as one of problems encountered in his application of TM in a tropical environment, but dismissed by Kucera and Barrett (1995) as unsubstantiated. In such cases we changed trees and used new sensors; damaged sensors were dried, cleaned, and tested for subsequent use. Insect damage was never encountered with CT or TM cameras internally. Some insects or rats ate exposed plastic parts of TM cameras. We did not try spraying an insecticide because we were afraid of unknown bias caused by the pungent odor and in a wet environment it was likely that the effectiveness would last for only a few days.
The metal parts of TM were more prone to rusts than those of CT, which were housed in an airtight container. The gradual rust of the metal components and growth of mold on the electronic board were less noticeable problems, but need extra attention in an application in a tropical environment. Nevertheless we lubricated the metal pins with a small amount of WD-40 and continued the usage with a little rust. Upon request TM manufacturer provided us with new metal pins with an instruction for local replacement. Such replacement of minor parts was not available with CT.

The observation that CT performance declined over time suggests that the efficiency and effectiveness of CT were intrinsic, independent of the researchers’ experience. The set-up specifications of CT were not flexible, so as the equipment became older the performance declined. TM performance improved over time, suggesting it was influenced by extrinsic factors such as specifications and experience. The importance of experience and training in using TM were emphasized by Kucera and Barrett (1995). Initially, when I was refining the technique, I changed the type of battery used in the cameras and the sensor sensitivity to improve trapping success. Because the premature exhaustion of the camera batteries was one of the main causes for the TM 0 functionality, choice of battery was important. I used either Duracell® or Energizer® brands. The lithium battery provided with the cameras were often old, and rechargeable alkaline batteries were depleted in a few days. Although expensive, the Duracell High Performance AA were better than regular AA, and the lithium 3-volt battery fresh from the shelf was the best. In TM, however, the lithium battery lasted on average 14 days whereas it lasted more than a month in CT. The rate of power drain was rather a function of susceptibility to humidity than the model of camera. Indeed, batteries in TM set up on ridge tops or other higher ground often lasted longer than ones in lowland because it was drier on the higher ground. As suggested by the manufacturer (B. Goodson, Goodson Associates, personal communication) and Hernandez et al. (1997), we cleaned the rubber O-ring of cameras monthly, first by blowing with high pressure air, and then if it was visibly dirty, swabbed with cotton dipped in isopropyl alcohol. Cameras set to “Fill-in”
flash mode, which would take every photo with a flash, were soon changed to “Auto” to save the power, which resulted in some dark images; nonetheless, identification of species or individual tigers were not compromised.

The relatively poor TM performance in MP was also due to the trigger system (TM Multi-camera Trigger II), which was used extensively in the first 2 months of the study to simultaneously trigger 2 cameras connected to 1 sensor. The device was especially susceptible to water and humidity. In the dry season in India, the trigger system works well just wrapped in plastic and buried underground (U. K. Karanth, Wildlife Conservation Society-India, personal communication). Even attaching the trigger system to the strap holding up the receivers did not help in our study. Our further attempts to waterproof the devise with silica gel, silicon glue, and plastic bags failed, and the use of the trigger system was discontinued.

Towards the end of the trapping at the first site, responding to an inquiry about the large number of nil photos, Bill Goodson, the manufacturer of TM systems, advised me of a technique for precise alignment of TM. We incorporated this into subsequent trapping sessions, which may have contributed to the slight improvement in TM performance.

Initially I chose the TM camera delay (i.e., the period between consecutive photographs) of the minimum setting of 6 seconds, with the hope of obtaining successive photographs of a tigress followed by her cubs. Yet, I have never obtained photographs of cubs despite sighting of such animals and presence of tracks. Karanth (1995) found that the capture probabilities of cubs were extremely low or even 0. At the beginning of trapping in the last study site (KK), a financial constraint required a higher trapping efficiency in a shorter time with a possible compromise and bias in data. Consequently, I changed the camera delay from 6 seconds to 12 seconds, which increased the number of trap nights by decreasing the number of consecutive nil photos. If consecutive photographs of the same individual or the same group of animals were not important to a study, I recommend a longer camera delay setting. Overall, experience and better specifications improved TM performance, but the rate of improvement was trivial, suggesting that
lack of experience or poor specifications were not the primary reasons for the poor performance of TM.

Yet another, but perhaps more important aspect for consideration in using TM from a project management perspective is the need for an immediate judgement when something goes wrong in the field. Extrinsic factors affecting the performance or malfunctioning components have to be identified and problems resolved. This involves quick assessment of a dozen factors affecting the performance and making a decision without compromising either data or resources. Replacing with a whole new set of equipment is easy if afforded, but if the problem were with the location (e.g., areas with high traffic of humans, elephants, and bats), then one had to decide whether to terminate the trapping, which wastes the effort to reach the site and possibly loses the data, or continue with modification, which risks the equipment and resources but possibly gains data. Because it often took us half a day or so to reach a trap site, we were reluctant to close the trap unless absolutely necessary. These kinds of troubleshooting and judgement could not be made by field staff who only knew how to set and check cameras. In addition, field technicians with limited formal education were not good with the sophisticated TM and all its settings and buttons. Lastly, the time spent on TM looking for a pair of suitable trees, setting up 3 components precisely on the trees, troubleshooting prone-to-malfunction units in the field and maintenance back in the field station was considerably longer than that for CT.

The CT system was relatively problem free. It was reliable, simple, easy to set up, and requires minimal experience and troubleshooting since the whole unit had to be replaced in case of malfunctioning. In fact, an identification of the malfunctioning component was not necessary since the whole unit had to be returned to the manufacturer for diagnosis and repair. CT withstood high humidity (with silica gels inside) as long as water did not enter the sensor through the mesh opening; animals slightly moving the system was not a problem; and many of the extrinsic variables did not affect performance except for playful elephants, vandalism, flood, and fallen trees.
One negative aspect of CT that could not be quantified, therefore not analyzed, was the sensitivity of the sensor to water. The sensor, housed in the bottom of the casing had a mesh opening through which water could enter. It seemed to be sensitive even to perspiration of the field crew (inside backpacks). Due to this, or perhaps other factors unknown to us, systems tested okay in the morning in a base camp sometimes would not function properly once we reached a trap location. Failing to function at the test shot was, however, far better than the 0 functionality of TM that occurred after the test shot. In any case we transported CT in a strong plastic bag, which was not necessary with TM, and we usually carried twice the number of CT deemed necessary if available. Alternatively, carrying a portable mini drier might be useful in drying the sensor before installation.

Camera trapping is a powerful but expensive technique to study rainforest mammals compared to the traditional approaches. Yet, despite the expense and some technical difficulties, the use of camera trapping is likely to continue and increase since there is no other method that produces the kind of incontestable evidence of secretive or low-density mammals produced by the technique. Because the initial investment on the equipment is high, it is important to select a system that produces the highest return for an investment in a selected environment. Although this paper focused primarily on 2 quantitative measures that were statistically testable, there are many other features of remote camera systems that deserve consideration before purchase as discussed above. Depending on application, some features are more important than others. For example, in this study, where it was logistically impractical to check cameras deployed in remote areas more than once a month, the reliability, portability, and resistance against unexpected extrinsic events were important. Water resistance is also vital for studies in rainforest habitats. Because of these special considerations required for an application in the rainforest environment, the inexpensive homemade camera units triggered by pressure plates (York et al. 2001) that worked well in USA (York et al. 2001, Moruzzi et al. 2002), for example, would not have been applicable in this study. The forest floor in the lowland forest frequently becomes inundated after
heavy rain; thus, any type of pressure plates would experience difficulty electronically during the flood and mechanically after the flood when the mud around and on the plates hardens (York et al. 2001).

Both manufacturers continue to modify and improve the products to cater to the needs of various consumers, which include researchers. One area needing improvements in all remote camera systems is portability. The basic design of TM and CT has not changed in the past decade while personal computer and television shrunk to a pocket size. Lasting power sources will continue to be the challenge for engineers. Researchers would save the cost of hiring porters and their maintenance if more compact and lasting power sources were made available even at a higher cost. The actual field camera maintenance work takes only 1-3 persons (for safety reason). Recent improvements are not discussed in this chapter; thus, I recommend researchers contact the manufacturers for the latest information or check out their WebPages (see Table B-1). The customer service of TM was superior and all contacts with TM manufacturer were timely, pleasant and informative while CT had much room for improvement in this area. Repair work done by CT was generally more costly and took longer than TM.
Table B-1
Specifications of the 2 remote camera systems tested in Taman Negara, Malaysia between 1999 and 2001.

<table>
<thead>
<tr>
<th>Trade name</th>
<th>TrailMaster (TM)</th>
<th>CamTrakker (CT)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Model</td>
<td>TM1500 sensor</td>
<td>Year 1999 model</td>
</tr>
<tr>
<td></td>
<td>TM35-1 camera</td>
<td>Camera included in the unit</td>
</tr>
<tr>
<td>Camera model</td>
<td>Olympus Infinity Mini DLX</td>
<td>Yashica T4 Super</td>
</tr>
<tr>
<td>Infrared sensor</td>
<td>Active</td>
<td>Passive</td>
</tr>
<tr>
<td>Cost (US$ as of 2001) (Exclusive of shipping and handling)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total</td>
<td>582.95</td>
<td>Total: 449.94</td>
</tr>
<tr>
<td>Sensor</td>
<td>260</td>
<td>CamTrakker: 429.99</td>
</tr>
<tr>
<td>Camera</td>
<td>290</td>
<td>Cable lock: 19.95</td>
</tr>
<tr>
<td>Cable lock</td>
<td>19.95</td>
<td></td>
</tr>
<tr>
<td>Casing</td>
<td>13.00</td>
<td></td>
</tr>
<tr>
<td>Weight (kg) (Inclusive of batteries and film)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total</td>
<td>2.70</td>
<td>Total: 1.90</td>
</tr>
<tr>
<td>Sensor</td>
<td>1.40</td>
<td>CamTrakker: 1.00</td>
</tr>
<tr>
<td>Camera</td>
<td>0.25</td>
<td>Cable lock: 0.50</td>
</tr>
<tr>
<td>Wire</td>
<td>0.10</td>
<td>Locking flange: 0.40</td>
</tr>
<tr>
<td>Casing</td>
<td>0.45</td>
<td></td>
</tr>
<tr>
<td>Power source</td>
<td>8 C-cell alkaline batteries</td>
<td>4 C-cell alkaline batteries</td>
</tr>
<tr>
<td>Warranty</td>
<td>12 months</td>
<td>6 months</td>
</tr>
<tr>
<td>Contact address</td>
<td>Goodson and Associates, Inc.</td>
<td>CamTrak South, Inc.</td>
</tr>
<tr>
<td></td>
<td>10614 Widmer</td>
<td>1050 Industrial Drive</td>
</tr>
<tr>
<td></td>
<td>Lenexa, KS 66215</td>
<td>Watkinsville, GA 30677</td>
</tr>
<tr>
<td>Set-up specification</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Focal distance</td>
<td>3-7m at 50 cm above ground</td>
<td>3-7 m</td>
</tr>
<tr>
<td>Camera delay</td>
<td>0.1 (6 sec) or 0.2 (12 sec)</td>
<td>3 minutes (the lowest setting)</td>
</tr>
<tr>
<td>Sensor sensitivity</td>
<td>4 (0.20 sec)</td>
<td>Not adjustable</td>
</tr>
<tr>
<td>Operational mode</td>
<td>Usually 24 hours; or 1700hr – 0900hr in high human traffic areas</td>
<td>24 hours; not used in high human traffic areas</td>
</tr>
<tr>
<td>Frequency of maintenance</td>
<td>Once a month</td>
<td>Once a month</td>
</tr>
<tr>
<td>Film</td>
<td>Fuji or Kodak 400 ASA 36 exp.</td>
<td>Fuji or Kodak 400 ASA 36 exp.</td>
</tr>
<tr>
<td>No. of units purchased</td>
<td>45</td>
<td>34</td>
</tr>
<tr>
<td>Total period of use</td>
<td>April ’99 – August ’01</td>
<td>Feb ’00 – August ’01</td>
</tr>
<tr>
<td>29 months</td>
<td>19 months</td>
<td></td>
</tr>
<tr>
<td>No. units returned for repair</td>
<td>14 sets (transmitters and receivers)</td>
<td>25 (16/year) b</td>
</tr>
<tr>
<td>(6 sets/year)</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

a TrailMaster does not provide a protective casing and locking device, thus they were designed and purchased separately.

b 12 of these were related to cameras. Therefore the attrition rate strictly of sensors was 13 units (8/year).
Table B-2
Descriptions and numbers of cases for 12 factors determined to be the causes for the “0 functionality” of TrailMaster (TM) and CamTrakker (CT) remote camera systems tested in Taman Negara, Malaysia, 1999-2001. The “0 functionality” involves cases where the system stops functioning prematurely and the data are either not retrievable or consisted entirely of “nil photos”. Nil photo refers to a photograph with no discernible image of wildlife.

<table>
<thead>
<tr>
<th>Description</th>
<th>TM (case)</th>
<th>CT (case)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Theft</td>
<td>2</td>
<td>3</td>
</tr>
<tr>
<td>Vandalized</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>Elephant</td>
<td>3</td>
<td>1</td>
</tr>
<tr>
<td>Moved</td>
<td>1</td>
<td>0</td>
</tr>
<tr>
<td>Faulty set-up</td>
<td>2</td>
<td>1</td>
</tr>
<tr>
<td>Film damage</td>
<td>6</td>
<td>2</td>
</tr>
<tr>
<td>Film advancing</td>
<td>0</td>
<td>8</td>
</tr>
<tr>
<td>Flooded</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>Blocking object</td>
<td>3</td>
<td>0</td>
</tr>
<tr>
<td>Camera battery</td>
<td>22</td>
<td>0</td>
</tr>
<tr>
<td>Malfunction</td>
<td>25</td>
<td>4</td>
</tr>
</tbody>
</table>

- **Theft**
  The system (or components of) was stolen and data not retrievable.

- **Vandalized**
  The system was vandalized by people, and data not retrievable.

- **Elephant**
  The system was damaged by elephants, and data not retrievable.

- **Moved**
  The system was moved by unknown forces (e.g., animals or falling objects), and thus became nonfunctional.

- **Faulty set-up**
  The system was set up improperly. This includes cases where CT or the camera of TM system aimed too high, the infrared beam of CT detected animals too far away to be effectively photographed, improper alignment of transmitter and receiver of TM system, vegetation interfering with the TM transmission, and the duct tape used to secure the TM sensors pealed off and covered the transmission or receiving window.

- **Film damage**
  The film was damaged by high humidity and condensation inside the camera. The chemical coating on the film became sticky and no images were retrievable.

- **Film advancing**
  Even when the sensor functioned and all components were powered properly, the camera failed to advance the film. This could be caused by at least 2 factors: 1) film was stuck inside the camera under conditions of high humidity (see above), and 2) forcefully pulling the stuck film out of the camera had damaged the film advancing motor of the camera. The Yashica camera in CT was especially susceptible to this. When the film was moderately stuck, the camera attempted to rewind the roll, and the camera LCD indicated that the entire roll of film had been exposed. When the film was tightly stuck, the camera could not rewind the film. To change the film in the field, we had to forcefully remove it and this action sometimes broke the Yashica camera. Film advancing motor of the Olympus camera (TM) rotated as film was removed.

- **Flooded**
  The system was flooded by rising water level.

- **Blocking object**
  The TM beam was intercepted by fallen objects such as trees, branches and large leaves.

- **Camera battery**
  Batteries in cameras almost always ran out before the batteries in sensors. The cameras of both TM and CT were set in stand-by mode, and power drain was greater under extremely humid conditions. In an area with low wildlife traffic, the battery died before the first event was registered.

- **Malfunction**
  A component of a system malfunctioned. When multiple components malfunctioned in TM it was difficult to ascertain which one failed first.
Table B-2 – continued.

<table>
<thead>
<tr>
<th>Description</th>
<th>TM (case)</th>
<th>CT (case)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Unknown</td>
<td></td>
<td></td>
</tr>
<tr>
<td>None of the above or more than 1</td>
<td>25</td>
<td>0</td>
</tr>
<tr>
<td>of the above and the main cause</td>
<td></td>
<td></td>
</tr>
<tr>
<td>could not be determined. Unknown</td>
<td></td>
<td></td>
</tr>
<tr>
<td>causes could include multiple</td>
<td></td>
<td></td>
</tr>
<tr>
<td>factors that could occur</td>
<td></td>
<td></td>
</tr>
<tr>
<td>simultaneously: 1) small animals</td>
<td></td>
<td></td>
</tr>
<tr>
<td>breaking the beam and moving</td>
<td></td>
<td></td>
</tr>
<tr>
<td>below the camera of the TM system,</td>
<td></td>
<td></td>
</tr>
<tr>
<td>2) sun effects, i.e., a direct and</td>
<td></td>
<td></td>
</tr>
<tr>
<td>abrupt reception of sun light by</td>
<td></td>
<td></td>
</tr>
<tr>
<td>the TM receiver causing 100s of</td>
<td></td>
<td></td>
</tr>
<tr>
<td>events, 3) animals detected by the</td>
<td></td>
<td></td>
</tr>
<tr>
<td>beam, but moved away quickly (e.g.,</td>
<td></td>
<td></td>
</tr>
<tr>
<td>bats and birds), 4) objects in the</td>
<td></td>
<td></td>
</tr>
<tr>
<td>focal range heated by the sun and</td>
<td></td>
<td></td>
</tr>
<tr>
<td>detected by CT, 5) movements of</td>
<td></td>
<td></td>
</tr>
<tr>
<td>small animals and invertebrates on</td>
<td></td>
<td></td>
</tr>
<tr>
<td>the TM transmission or receiving</td>
<td></td>
<td></td>
</tr>
<tr>
<td>window triggering false events, 6)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>poor electric conductivity due to</td>
<td></td>
<td></td>
</tr>
<tr>
<td>rusted parts, 7) obscure defects</td>
<td></td>
<td></td>
</tr>
<tr>
<td>in the system not easily detected</td>
<td></td>
<td></td>
</tr>
<tr>
<td>(e.g., electronics), and</td>
<td></td>
<td></td>
</tr>
<tr>
<td>8) other unknown extrinsic factors</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Figure B-1
Two types of remote camera systems tested in Taman Negara National Park, Malaysia, 1999-2001: CamTrakker® (CT) passive infrared system (above) and TrailMaster® (TM) active infrared system, showing the camera in the custom made casing (middle) and receiver (bottom). The TM transmitter is attached to an opposite tree, not shown here. The 2 systems were set up together for an intensive performance test. The tree shown here is relatively small compared to ones usually selected to set up camera traps. Thorny trees such as these (left) were often put against a tree and tied with a liana to prevent animals from brushing their bodies against a TM system while moving. A slight shift in TM sensor alignment would result in mis-firing the camera to take photographs of nothing.
Figure B-2
Proportions of the photographs produce by TrailMaster (TM) and CamTrakker (CT) remote camera systems for rainforest mammals in Taman Negara, Malaysia, 1999-2001. Number of photographs for mammalian species with more than 10 records were normalized with total trap nights of a particular system for comparison. The species are in descending order by the body size.
The comparison of overall performance, showing the total trap nights and types and numbers of exposures made with the TrailMaster (TM) and CamTrakker (CT) infrared remote camera systems at 3 study sites: a) Merapoh (MP), b) Kuala Terengan (KT), and c) Kuala Koh (KK) in Taman Negara, Malaysia, 1999-2001. Nil photo refers to a photograph with no ascertainable image of wildlife. The numbers of total trapping sessions at each site are in the parentheses.

Figure B-3
Figure B-4
Per trapping-session performance of TrailMaster (TM) and CamTrakker (CT) remote camera systems in Taman Negara, Malaysia, 1999-2001. The error bar represents ±1 standard deviation of the site-specific results. The numbers of the total trapping sessions are in the parentheses. Nil photo refers to a photograph with no ascertainable image of wildlife.
Figure B-5
Per trapping-session average trap nights of TrailMaster (TM) and CamTrakker (CT) remote camera systems at 3 study sites, Merapoh (MP), Kuala Terengan (KT), and Kuala Koh (KK) in Taman Negara, Malaysia, showing a slight increase in average trap night for TM and decrease for CT over time. The error bar represents 1 standard deviation of the site-specific result. MP, KT, and KK were sampled during May1999-May2000, March 2000-January 2001, and October 2000-August 2001, respectively.

Figure B-6
Monthly success rates of TrailMaster (TM) and CamTrakker (CT) remote camera systems in Taman Negara, Malaysia, showing a slight increase in the success rate for TM and decrease for CT over time. The sharp decline in the success rate for CT in February 2001 was due to malfunction of 2 out of 3 CT units.
Figure B-7
Comparison of causes for “0 functionality” between TrailMaster (TM) and CamTrakker (CT) remote camera systems tested in Taman Negara, Malaysia, 1999-2001. The “0 functionality” involves cases where the system stops functioning prematurely and the data are either not retrievable or consisted entirely of “nil photos”. Nil photo refers to a photograph with no discernible image of wildlife. See Table B-2 for description of each category. The pie chart depicts malfunctioning components of the TM system.
Figure B-8
Total trap nights, types and numbers of exposures made with TrailMaster (TM) and CamTrakker (CT) remote camera systems during the intensive performance test in Taman Negara, Malaysia, 2000. The numbers of total trapping sessions are in the parentheses. Nil photo refers to a photograph with no ascertainable image of wildlife.
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BIOGRAPHICAL SKETCH

Kae Kawanishi was born on January 3, 1968, in Osaka, Japan. She moved to the USA in 1985 to study wildlife conservation. She received a B. S. in animal ecology from Iowa State University and M. S. in applied ecology and conservation biology from Frostburg State University in western Maryland. Her thesis work involved a study of human impacts on rainforest mammals using camera traps in Tikal National Park, Guatemala. In the interim, she fell in love with America’s National Parks and volunteered in Mt. Rainier National Park in Washington and Assateague National Seashore in Maryland. She now volunteers for the Department of Wildlife and National Parks in Peninsular Malaysia. She hopes to work as a liaison between international organizations and local government authorities for research and conservation of rainforest ecosystems, using mammalian top carnivores as landscape species.