Jaguars as Landscape Detectives for the Conservation of Atlantic Forests in Brazil

by

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Dedication

In dedication to the loving memory of my father Laury Cullen (1934-2002)

(Photo by Laury Cullen Jr.)

" the jaguar was sent to the world

as a test of the will and integrity

of first humans"

(Colombian indigenous myth, Davis 1996)

Abstract

In this thesis, I show how the jaguar *Panthera onca* can be used as a landscape detective. A landscape detective is defined as a species that helps determine how to manage landscapes and to design and manage protected area networks. Life history and behavioural features of jaguar make them potentially suitable as landscape species. The main aim of this study is to use the jaguar as a landscape detective to develop a network of core protected areas for the Upper Paraná Region, which lies in the highly threatened Atlantic Forest of Brazil. Information was collected on jaguar density and home range, which was combined with habitat requirements of the species and GIS-generated maps of land cover to develop a map of habitat suitability. This map was used to understand the spatial structure of the jaguar metapopulation, identifying habitat patches of high suitability where jaguar populations exist and are likely to survive over the long-term. Camera trapping and capture-recapture models were used to derive jaguar population size in Morro do Diabo State Park (MDSP). Camera trapping was carried out simultaneously with VHF and GPS telemetry to verify density estimates. Jaguar densities were estimated to vary between 2.47/100 km^2 and 2.20/100 km^2. Jaguar home ranges and movements were also studied for 10 individuals in MDSP and Ivinhema State Park (ISP). In MDSP the yearly 85% fixed-kernel home range averaged 162 km^2 for male jaguars and 60 km^2 for females. In ISP the only male monitored had a yearly 85% home range of 147 km^2, while two females monitored averaged 130 km^2. Dry season 85% home ranges were similar to wet season home ranges. Female home ranges overlapped between 15 to 25%, while males overlapped on average 32%. Mean annual and multiyear 85% home ranges were larger than those reported by previous studies. The mean yearly distances between consecutive locations for all 10 individuals studied averaged 2.76 km. On average, jaguars moved similar distances in the wet to the dry season (2.85 to 2.40 km/day). The average maximum distance moved by any jaguar between consecutive locations was 13.18 km/day. Occasionally 30 km movements were recorded when male jaguars traversed open pastures and gallery forests over very short periods. Using compositional analysis, I assessed habitat selection by jaguars at second- and third-orders of selection. At second-order selection, jaguars consistently preferred primary forests and dense marshes, and avoided human-dominated areas such as intensively managed open pastures. Although the avoidance of disturbed and developed habitat types by jaguars is not surprising, this is the first study to document such evidence. At third-order selection, jaguars concentrate their core areas in areas of high prey density, whether wild herbivores or livestock. With this information, I developed the landscape detective model to help identify strategic transit refuges or stepping stones for dispersing jaguars that could improve the dispersal potential of corridors between suitable habitat patches. The model produced a habitat suitability map and patch structure with 3 suitable patches having a total area of over 4,000 km^2 and a carrying capacity of 126 jaguars in the Upper Paraná Atlantic Forest. The habitat-based landscape detective model was linked to a population viability analysis. Under the "current" scenario, the metapopulation tended to decrease. The median time to decline to half of the initial abundance, from 126 to 63 jaguars, was about 18 years, while the risk of extinction within the next 50 years was predicted at around 25%. However, the results under a predicted "protection" scenario were quite different showing a stable metapopulation with a low risk of extinction, a high predicted abundance and a high occupancy. The results of the model can help develop agroforestry programmes to improve habitat quality of potential wildlife corridors and buffer zones. The findings of this thesis show how a landscape detective species can be used to improve landscape management and protected area networks. If the jaguar is to have a chance of surviving in future human dominated landscapes, protected area management will need to integrate applied research with good policies for the involvement of NGO and Universities, co-management of protected areas, participation of local communities through community-based landscape restoration programmes, and environmental education.

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CHAPTER 1

INTRODUCTION

Successful and effective strategies for biodiversity conservation must meet the needs of wildlife and people in biologically functioning and increasingly human-dominated landscapes. Isolated protected areas have had an increasing impact in protecting elements of biodiversity that promotes nature conservation (Redford and Richter 1999, van Schaik et al. 2002, Redford et al. 2006). In most places where protected areas are declared, strict and full protection is not always possible over large areas. In turn, protected areas fail to conserve all elements of the natural biota. Most protected areas occur in a landscape where a wide range of natural resource exploitation occurs (Brandon et al. 1998, Putz et al. 2001, Bodmer and Robinson 2004). Effective conservation will have to integrate responsible use of resources by local communities, strict protection, and law enforcement across the conservation landscape. Such an approach must integrate different types of land uses such as urban areas, agriculture zones, concessions, buffer zones and strictly protected areas such as national parks (Kramer et al. 1997, Redford et al. 2006). The establishment and management of protected areas and functioning landscapes with different types of land uses is one of a variety of methods promoted to help conserve biological diversity.

Within these landscapes, the need for strictly protected areas with suitable habitat patches has been increasing emphasized for an array of species and components (Redford and Richter 1999). However, few systematic methods have been proposed to help in mapping and designing the conservation landscape. In designing a protected area or a protected area network, a regional system of protected areas), conservationists generally use some combination of three approaches. These approaches are: 1) mapping special elements (i.e., sites of high value such as wilderness areas, road-less areas, and location of rare species), 2) seeking representation (i.e., including all habitat types in a region as a “coarse filter” approach to protecting biodiversity), and 3) evaluating the requirements of selected focal species (Noss 1996, Sanderson et al. 2002, Coppolillo et al. 2004). Relying on only one of these approaches will not provide sufficient protection, so understanding the strengths and weakness of each approach should aid decisions about integrating them into a more comprehensive protected area plan.

Because it is impossible to inventory every species in an ecosystem, scientists usually concentrate on a few key or focal species. Definitions of different types of focal species appear widely in the literature (Leader-Williams and Dublin 2000). Some species play a critical role in regulating the health of an entire ecosystem and their impacts on community or ecosystem structure are greater than would be expected from their relative abundance. These species are known as *Keystone Species* (Paine 1980, Terborgh 1988, Mills et al. 1993, Miller et al. 1999). If wide ranging species at the top of the food chain have enough area to maintain viable populations, the chances are that other species also will be protected. These species, whose areas of occupancy or home range are large enough that they will bring other species under their protection, are known as *Umbrella Species* (Lambeck 1997). Because it is also important to know whether a conservation plan is working, scientists look for species whose health reflects that of the surrounding ecosystem. Changes in the distribution, abundance and demographic characteristics of such species may indicate impeding adverse changes in the ecosystem as a whole. In scientific terms, these are known as *Indicator Species.* Finally, popular and charismatic species that could serve as symbols and leading elements to promote conservation awareness and action are know as *Flagship Species* (Bowen-Jones and Entwistle 2002)

The use of selected species as a basis for site-based conservation has been widely used for designing landscape conservation. For example, Lambeck (1997) presents a multi-species approach for defining the attributes required to meet the needs of the biota in a landscape and the management regimes that should be applied. His approach builds on the concept of umbrella species, whose requirements are believed to encapsulate the needs of other species. It identifies a suite of “focal species,” each of which is used to define different spatial and compositional attributes that must be present in a landscape and their appropriate management regimes. For each relevant landscape parameter, the species with the most demanding requirements for that parameter is used to define its minimum acceptable value. Because the most demanding species are selected, a landscape designed and managed to meet their needs will encompass the requirements of all other species. Miller et al. (1999) present some ideas for using focal species in conservation action. They discuss the role of focal species in planning a reserve network and define focal species as “organisms used in planning and managing nature reserves because their requirements for survival represent factors important to maintaining ecologically healthy conditions”. Sanderson et al. (2002) provide a conceptual methodology for landscape conservation that is being tested by the Wildlife Conservation Society at three sites in Latin America and Africa. The biological landscape is defined as the biological requirements of an ecologically functioning population of a landscape species. This landscape is then compared to the landscape of human activities through the use of a Geographical Information System (GIS). Focal landscapes sufficient to meet species requirements are defined and threats from human activities evaluated with respect to biological requirements. A suite of landscape species may be selected depending on resources, leading to multiple, often overlapping focal species.

Coppolillo et al. (2004), define five criteria for selecting landscape species comprising area requirements, heterogeneity, ecological function, vulnerability, and socioeconomic significance. These authors illustrate the process using data from two landscapes, the north-western Bolivian Andes and northern Congo. Candidate species from each site are scored and suites of complementary landscape species are assembled. These authors emphasize that, like all focal-species approaches and, indeed all conservation planning, their approach is not without biases. By making explicit assumptions and allowing evaluation of the inherent biases, they attempt to provide a transparent, replicable method for identifying species around which to structure site-based conservation known as landscape species. The process is also useful for identifying data gaps, ranking threats, and setting research priorities.

Redford et al. (2003) provide a conceptual comparison of some approaches currently being implemented by conservation organizations. They examined these approaches according to the nature of the conservation target, the question addressed, the scale of the approach and the principles that underlie the approach. They conclude that only with an explicit understanding can the conservation community and its supporters critically compare approaches and come to a consensus about a set of metrics for measuring and achieving global conservation. Among most of the approaches compared, the authors emphasize the need of using focal species, especially large predators, in the design of nature reserve networks.

1.1 Top Predators as Focal Species

Many top carnivores are keystone species essential to the maintenance of biological diversity and promotion of long-term ecosystem integrity (Soulé and Noss 1998). Examples of keystone carnivores that significantly regulate ecosystem processes include the beaver, *Castor canadensis* (Naiman et al. 1998), large carnivores (Terborgh 1998) and prairie dogs, *Cynomys* spp. (Miller et al.1994). Protection of keystone species gives managers a value and an avenue to educate the public about the relationship between the various parts of an ecological system (Leader-Williams and Dublin 2000).

Large carnivores, by definition, can also act as umbrella species. Despite functional differences, it is possible to choose species that occupy more than one definition. For example, top carnivores such as grizzly bears (*Ursus arctors*) and jaguars (*Panthera onca*) could be both keystone species and umbrella species because of their large area requirements. Protecting enough habitats to assure viable populations for grizzlies and jaguars would probably benefit many other species more restrict in their range.

Examples of carnivores as indicator species also have appeared in the literature. Mountain lions (*Puma concolor*), bobcats (*Lynx rufus*) and grey foxes (*Urocyon cinereoargenteus*), have been used as plague indicators in California, USA (Smith

1994). These carnivores routinely consume rodents as a part of their diet. In nature the bacteria that cause plague, *Yersinia pestis*, cycles between several rodent species and their fleas. When these carnivores capture and eat these rodents they can become infected with plague. By sampling carnivore blood, one can obtain data that provides a picture of plague activity in a given area. This effort utilizes blood samples from carnivores as indicators for plague.

Flagships such as tigers (*Panthera tigris*) and the Komodo dragon (*Varanus komodoensis*) have also been used by international conservation organizations to raise public awareness and fundraising for conservation projects in developing countries (Leader-Williams and Dublin 2000, Walpole and Leader-Williams 2002). Funds may be used through awareness campaigns that focus on these flagships as symbols for the natural environment. For example, the Komodo dragon, confined to the islands of Komodo National Park, is valued as an important flagships species through tourism in this area. Although established to conserve the dragon, the Park also protects other endangered species. The Komodo dragon attracts a large number of western visitors to an otherwise little-known area of Indonesia. Visitors spent over US$1,000,000 in the surrounding community in 1995/1996, supporting over 600 jobs and providing direct benefits to over 30% of the local population (Walpole and Goodwin 2000). As a result, the local population generally held a positive attitude towards Komodo National Park, recognizing the role of the dragon in attracting tourists, and supporting local conservation.

In addition to providing a useful lens for defining conservation landscapes, large carnivores can also play an important role in regulating terrestrial ecosystems. Large carnivores are keystone species that make substantial contributions to ecosystem function. Excluding them may result in a protected area with highly altered and unstable systems (Terborgh 1998, Terborgh 2005). Although there is intense debate over the issue of "top-down" versus "bottom-up" process, there is increasing evidence that many ecosystems are regulated from the top by large keystone carnivores, that ecosystems may collapse or be radically altered without them, and that diversity and resilience will be lost as a result (Steneck and Sala 2005, Terborgh 2005). "Top-down" means that species occupying the highest trophic level, such as top carnivores, exert a controlling influence on species at the next level, their prey, and so forth down the trophic ladder. Terborgh (1999) shows evidence supporting the "top-down" versus "bottom-up" process.

Different types of evidence are categorized as anecdotal, where controls are lacking, or experimental with well controlled comparisons. Among the anecdotal examples are herbivore releases onto predator-free islands (Klein 1968, Carlquist 1974, Bowen and van Vuren 1997), predator elimination and the Paine's effect (Paine 1966, MacShea et al. 1977), predator introductions (King 1984, Bayley 1993, Hatter and Janz 1994), and long-term monitoring of predator/prey interactions (MacLaren and Peterson 1994, Messier 1994, Estes 1996). Among the experimental examples for "top-down" processes are the cases of Barro Colorado Island in Panama, the Lago Guri Islands in Venezuela, and more recently in Zion National Park, USA. The hyperabudance of persistent vertebrates in these areas is consistent with the top-down effect of release from predation (Terborgh 1988, 1992, Wright et al. 1994, Terborgh et al. 1997, Terborgh 2005, Ripple and Beschta 2006). Bowyer et al. (2005), discuss various systems without large carnivores that often experience trophic cascade, in which ungulates have deleterious effects on vegetation and other animals. These studies suggest that where key predators such as large mammalian carnivores have been removed, some consumers tend to increase in density, for example increased wild ungulate populations or high densities of domestic ungulates and have a significant impact on native species diversity.

A careful selection of umbrella and habitat indicator focal species can be useful in the design and implementation of protected area networks. Focal and top predator species are also important in regulating terrestrial ecosystems. Therefore, efforts to conserve large tracts of wildlands in interconnected protected areas will have to place a high priority on species whose life history characteristics, trophic role and biological requirements in space and time make them particularly useful for landscape planning and biodiversity conservation.

1.2 Jaguars as Landscape Detectives: The Concept

A large-scale approach to nature conservation calls for large, connected core areas with their full complement of native species (Soulé and Noss 1998). The central goal of this approach is to maintain or restore ecologically viable populations of large carnivores and other keystone species (Soulé and Terborgh 1999, Foreman and Daly 2000, Ray 2005). This thesis proposes to use the jaguar as a landscape detective, given the jaguar's ecological significance and need for extensive areas of secure, high-quality habitat. By definition a "Detective" is …"*a private investigator whose function is to obtain information and evidence…*or *someone engaged in getting and or detecting information that is not readily or publicly accessible*" (dictionary.com). Landscape detective species can be defined as organisms that can help obtain information and evidence from fragmented landscapes on how to design and manage protected area networks, because their requirements for survival show us factors important to maintaining large core and connected landscapes in ecologically healthy conditions. More specifically, the main goal of this work is to use the jaguar as a landscape detective to develop a network of wild core reserves for the Upper Paraná Region in Brazil.

I developed the landscape detective approach by working with top keystone species such as the jaguar, in combination with GPS telemetry, GIS-generated landscape data, habitat suitability functions and population modelling. This approach uses information on density and home range, combined with habitat requirements of the species and GIS-generated maps of land cover, and combines these data into a map of habitat suitability (HS) with a habitat function. This map is then used to find habitat patches by identifying areas of high suitability where jaguar populations exist and might survive over the long-term. This approach should be considered a tool that can help managers to build species and landscape conservation models, and then to link spatial data with population viability analysis for species.

The landscape detective approach is closely related to other focal species focused conservation planning techniques such as umbrella species, keystone or flagship species (Lambeck 1997, Caro and O'Doherty 1999, Miller et al. 1999, Sanderson et al. 2002). These approaches choose certain species whose life history characteristics and biological requirements in space and time make them particularly useful for identifying when and where human uses of the landscape may compromise ecological integrity of the overall landscape (Sanderson et al. 2002). Examples where large carnivore species have been used as focal species for planning in terrestrial habitats include habitat and distribution modelling (Carroll et al. 2001), conservation area design (Mills et al. 2001, Carrollet al. 2003), spatially explicit population viability modelling (Noss 2000, Carroll et al. 2003) and evaluation of landscape permeability (Singleton et al. 2002).

The landscape detective approach has also certain special features. First, the landscape detective approach was developed for jaguar populations that still remain in highly fragmented habitats. Central in this approach is to use the jaguar to detect core areas and isolated patches and stepping stones habitats for landscape restoration and metapopulation conservation. Other approaches such as the umbrella species do not seem to relate specifically to enhancing connectivity, linkages and defining specific lands and areas for restoration. Also, the landscape detective is more species-intrinsic in that the species habitat relationship is the central point to this approach. In the landscape detective approach, species-habitat requirements provided by habitat selection analysis are used to build a habitat suitability function to define the landscape in which conservation must occur.

Furthermore, the jaguar is also a very charismatic species in many regions in which the species occurs, and conservation organizations, donors and local people were willing and prepared to pay for the charisma. In this way, the combination of terms of "jaguar" as "landscape detective" was also used to strategically draw financial support and to raise funds more easily. By doing so, the jaguar could help to protect many other species in its habitats.

Other approaches seem more species-extrinsic. For example, Sanderson et al. (2002), describe their focal species conceptual model as “the lens through *which we* view the landscape to determine where conservation must occur”. In contrast, the landscape detective approach attempts to identify habitat patchiness from a species point of view, and tries to determine how the species itself perceives the patchiness of the landscape. Second, the landscape detective approach goes beyond the conceptual framework and provides the tools for managers to build their own model with other focal species in conservation planning based on landscape species requirements.

If terrestrial carnivores are used as focal species and landscape detectives, I recommend, when possible, more emphasis on females. Male carnivore movements can be extensive, highly variable and related mainly to social status, behavioural spacing mechanisms, and hormonal production (Ewer 1973, Powell 1979). For example, the male weasel’s (*Mustela erminea*) territorial system breaks down during the breeding season, and a class of super males range far beyond their usual home range areas to reproduce (Sandell 1986). Female carnivores, on the other hand are more valuable demographically and will raise their young in areas where critical resources are concentrated and easier to obtain (King 1989, Miller et al. 1996). They need to satisfy elevated energy requirements with minimal time away from their young, so they are more restricted to optimal habitat and their home range sizes more accurately represent the quality of that habitat (Lindstedt 1986, King 1989). For those reasons it is probably more practical to rely heavily on female movements and spatial needs when using focal species in landscape conservation.

1.3 Jaguars as Landscape Detectives for the Upper Paraná Region

The Upper Paraná Region is an appropriate landscape to test and apply the landscape detective approach with the jaguar. This region strategically connects large protected areas along the Paraná River, including the Iguaçu National Park in Brazil and Argentina. These areas are considered important for research and conservation efforts on jaguar populations due to their long term conservation prospects and ecological peculiarities. Jaguars may exhibit a metapopulation structure in the Upper Paraná region. A metapopulation is defined as a “network of isolated and semi-isolated populations with some level of regular or intermittent migration and gene flow among them, in which individual populations may go extinct but can then be recolonized from other populations“ (Meffe and Carroll 1997).

The extinction risk of a single population is determined by factors such as population size, life history parameters and demographic and environmental stochasticity that cause variation in these parameters. The extinction risk of a metapopulation or a species depends not only on the factors that affect the extinction risk of each population, but also on other factors that characterize interactions among these populations (Akçakaya 2005). Among other additional factors that operate at the metapopulation or species level are the number and geographic configuration of habitat patches inhabited by local populations. By applying the landscape detective approach, it is then possible to determine the spatial structure of the jaguar population in the study region and produce a spatial metapopulation scenario of the Upper Paraná jaguar populations.

The main hypothesis is that by using jaguars as landscape detectives we can identify and assess three important and independent features that characterize large carnivores and large scale conservation planning: (1) prey diversity and density, (2) large core areas and important habitat patches for biodiversity conservation, and (3) landscape connectivity. Two major scientific arguments constitute the landscape detective approach and justify the emphasis on large predators, such as jaguars:

1) Large core areas: wide-ranging predators usually require space and large cores of protected landscape to secure prey, seasonal movement, and other needs. By studying and comparing jaguar distribution and density in specific locations it should be possible to detect core sections or habitat patches for the network of conservation areas. These areas should protect wild habitat, biodiversity,

ecological integrity, ecological services, and evolutionary processes in the Upper Paraná-Paranapanema ecosystem.

2) Landscape connectivity: connectivity is also required because core protected areas are typically not large enough in most regions and they must be linked to ensure long-term viability of wide-ranging species. By tracking young dispersing jaguars that use forest patches as links in the fragmented landscape, the landscape approach should be able to detect key and potential linkages between large natural areas. This could ensure the continuation of migrations and other movements vital for the survival of the metapopulation.

Landscape conservation planning emphasizing the jaguar as a landscape detective offers a novel approach to protected area design. This is an approach that uses the jaguar to determine landscape conservation, which in turn should conserve the entire ecosystem, since top carnivores require prey, large core areas and connectivity. It is certainly a major step above some current practices that include looking at a satellite image in an office and guessing where a core reserve, a habitat patch or a corridor should be. I am not proposing using a landscape detective approach as a surrogate for all species of concern. However, in the Upper Paraná Region, management decisions can not await the conclusion of long-term studies on more sedentary species. In this region, the use of data from GPS radio collared jaguars may be the most practical way to integrate biological information into the analysis of fragmentation and the mitigation related to wildlife management, landscape ecology, and planning.

1.4 Previous Jaguar Research

Few studies have investigated the biology of the jaguar (*Panthera onca*) until recently. This is remarkable, considering that the jaguar is the world's third largest species of living cat and the largest cat in the Americas. Its geographic distribution covers a considerable part of Mexico, all of Central America, and South America as far as northern Argentina. The exception to this is Uruguay where it has been extinct since the early 1900s, and the south-western United States where it is found only on the United States-Mexico border (Swank and Teer 1989, Nowak 1994, Brown and Gonzales 2001). Information preceding 1970 when available consists mainly of anecdotes and notes on the animal's natural history (von Humbolt 1852-53; Rengger 1830; Roosevelt 1914; Miller 1930; Leopold 1959; Brock 1963; Mondolfi and Hoogesteijn 1986).

Since 1970, a number of studies have been published on the jaguar. A study of the adaptive differences in the body proportions of large felids was undertaken by William J. Gonyea (1976) who compared body proportions in eight large felids, including the jaguar, to determine whether functional differences due to morphological variation could be correlated with different behavioural and ecological strategies. Later, Schaller and Crawshaw (1980) undertook what is considered by many to be the first serious study of jaguar distribution using radio telemetry at the Acurizal Ranch in the Pantanal Region, State of Mato Grosso, Brazil. The status of the jaguar in the south-western United States was investigated by David E. Brown of the Arizona Game and Fish Department (1983). His paper dealt with a historical overview of jaguars that had been killed in Arizona and New Mexico and the resulting long-term population dynamics. Further study of the ecology and behaviour of the jaguar was conducted in the Cockscomb Basin of Belize by Rabinowitz and Nottingham (1986). The first comprehensive paper on the biology of the jaguar as a whole was presented by Mondolfi and Hoogesteijn (1986). Their study of the biology and status of the jaguar in Venezuela was the first to integrate all aspects of the jaguar's biology into a concise format. This is not to say Schaller's work (1978-1980) is not significant; his was the first in-depth field work of a scientific nature performed with the jaguar and still remains the standard by which all other research work is judged for this species. Finally, Jaguar research in the Neotropics had a great input with the publication of the book "Jaguars in the New Millennium" with a collection of chapters on jaguar biology across Latin America (Medellin et al. 2002). It should also be noted that the Wildlife Conservation Society (WCS) has historically underwritten several field expeditions devoted to the *in situ* study of the jaguar (Schaller and Crawshaw 1980, Rabinowitz and Nottingham 1986, Cavalcanti 2004, Maffei et al. 2004, Silver et al. 2004, Marieb 2005, Soisalo and Cavalcanti 2006, Weckel et al. 2006).

Humans also persecue of jaguars as a result of their depredation of livestock, or because of the potential danger that these animals represent to human life. Retribution killings are the final step in the process of disappearance of jaguars outside protected areas, a process that begins with the loss and fragmentation of habitat (Nowell and Jackson 1996). Jaguars demonstrate an enormous adaptability in their dietary habits, and domestic animals, especially cattle, constitute and important part of the jaguar's diet, especially in their floodplain areas distribution (Crawshaw and Quigley 1984; Hoogesteijn and Mondolfi 1992). Publications summarized by Oliveira (1992), and Hoogesteijn and Mondolfi (1996), compare the diets of jaguars in rainforest zones with that of jaguars in areas of flooded savannas. These show that domestic animals, especially cattle, constitute an important item in the jaguar's diet in floodplain areas. In Costa Rica, Hoogesteijn and Mondolfi (1996) report significant losses caused by jaguar depredations on small cattle ranches (a total of $60,000 US dollars between 1991-1998) with losses of some $1.125 US dollars per rancher. Hoogesteijn et al. (1993), determined the causes of death on three cattle ranches on the Venezuelan Llanos and found that on the first ranch, Hato Piñero, deaths caused by felines were considerably fewer than those occasioned by other causes, reaching only 6% of total deaths or losses. A conservation strategy for the jaguar, in order to be successful must resolve the conflicts between jaguars and ranchers (Zimmerman et al. 2005). This conservation strategy in conflict resolution should aim in providing ranchers with information that allows them to understand that the problem of depredation does not constitute an isolated phenomenon. Rather, is a consequence of various factors that are important to understand; how to identify the animal responsible for the depredation; what steps to take in the management of their herds to diminish its occurrence; to provide possible solutions to the management of problem jaguars, and achieve a better coexistence between cats and the fauna.

1.5 Prior Jaguar Research in Brazil's Upper Paraná Region

Research related to jaguars in the Upper Paraná Atlantic Forest in Brazil began in 1990 with Peter Crawshaw´s study on the comparative ecology of jaguars and ocelots (*Leopardus pardalis*) in Iguaçu National Parks of Argentina and Brazil

(Crawshaw 1995). This study provided estimates of home range size for jaguars, described their diet and identified some important threats for this jaguar population. The study area of Crawshaw´s study constitutes the best protected area of this region and has a good prey base (Paviolo et al. 2005). Results of this study may not be representative of the region as a whole and may not be used to extrapolate jaguar densities to other areas. Since 1997, the Argentine National Parks Administration has conducted research to evaluate the effect of jaguar predation on cattle in a neighbouring area to the Iguaçu National Park. Schiaffino (2002) evaluated the effect of electric fences to reduce jaguar attacks on domestic animals and the association between jaguar attacks and different livestock management practices.

In 2002, Augustin Paviollo conducted a study to compare the availability of prey between the Iguaçu National Park and a nearby property where there is no control of hunting. He found a higher density of prey in the protected area, indicating that there could be spatial differences in jaguar abundances if prey is a limiting factor for the species (Paviolo, 2002). Most forest areas in the region are not protected, or if they are, they do not have proper management plan (Di Bitetti et al. 2003).

Since October 2002, Fundación Vida Silvestre Argentina (FVSA) with other institutions including the National Parks Administration of Argentina, the Ministry of Ecology and Natural Resources of Missiones and researchers from the Brazilian Institute for the Environment (IBAMA) has developed a Jaguar Conservation Program for the Green Corridor of Missiones. FVSA, under the coordination of Dr. Mario Di Bitetti, has begun two studies to determine the population status of jaguars in the Upper Paraná Atlantic Forest region and to obtain basic information to design a conservation landscape using the jaguar as an umbrella species. One of these studies is being carried out by Carlos De Angelo and has as its main objective to map the distribution of jaguars in the Upper Paraná Atlantic Forest Ecoregion and to establish a network of volunteers to monitor this population in the different forest remnants of this Ecoregion in Argentina, Brazil and Paraguay.

The jaguar has been declared Provincial Natural Monument in Missiones Province by law n° 2589 in 1988, and National Natural Monument by national law n° 2563 in 2001. This is the highest protection status that a species can enjoy in Argentina. In spite of this listing, no actions are being implemented to effectively protect the species. However, these laws demonstrate the interest of Provincial and National authorities to protect the species. Recently, a technical team from FVSA and the World Wildlife Fund (WWF) identified as a priority to ensure the long-term viability of umbrella species in the Upper Paraná Atlantic Forest Ecoregion (Di Bitetti et al. 2003). Jaguars, as top predators play an important role in maintaining healthy ecosystems through their top-down regulation of the population structure (Miller and Rabinowitz 2002). As an umbrella and landscape species, jaguars are very useful to design a biodiversity conservation landscape. FVSA and other institutions have promoted the creation of the Jaguar Committee, a group that advises the provincial government in the management and conservation of this species. Despite these efforts, there are still good estimates of the present jaguar distribution and its population size in the region. The only PVA conducted on this population was based on overly optimistic data of habitat availability and jaguar population parameters (Eizirik et al. 2002).

In 2006, an initiative led by Dr. Joanne Earnhardt from the Alexander Centre for Applied Population Biology, Conservation and Science, Lincoln Park Zoo, USA, in partnership with the Government of Argentina started to conduct a Risk Assessment of the Missiones, Argentina jaguar population. This initiative is combining life-history data from captivity with the specific landscape of the Missiones province, one of the last areas to support jaguars in Argentina, to create a spatially-explicit, individual-based population viability analysis model. The model's structure, like the data modification, arose from a series of meetings with field biologists and park managers. The model will serve as a tool to assess the Missiones population viability and to help identify management options that best maintain or improve the population's probability of long-term persistence.

1.6 This Thesis

Within the western Atlantic Forest range, the Pontal do Paranapanema Region, together with the Upper Rio Paraná ecosystem still maintains approximately 5.000 km^2 of relatively semi-connected and well-preserved semideciduous Atlantic Forests, including associated marshlands. This landscape is considered among the few areas where large carnivores such as jaguars, pumas and ocelots might persist (Sandenson et al. 2002) (Figure 1.1). Jaguars are relatively common in the Pontal region (Cullen et al 2000) and empirical information about their density, prey and habitat requirements, dispersal and metapopulation structure are needed to develop a landscape analysis of their metapopulation based on robust and field species-specific natural history information.

From 1997 through 2004, I investigated the jaguar ecology in the Morro do Diabo State Park. The project was extended to the Ivinhema State Park in the neighbouring Mato Grosso do Sul State, separated by the Paraná River. The study in Ivinhema State Park is still underway and is being carried out in cooperation with Pró Carnívoros Institute, and more specifically with Dênis Sanna. Together, through this extended and long term study of the natural history of the jaguar we are evaluating the species conservation prospects in Ivinhema and the surrounding landscape.

In this dissertation, Chapter 1 sets the stage for the landscape detective approach and reviews previous jaguar research in the Neotropics. Chapter 2 presents a brief description of the study areas and the Upper Paraná River.

In Chapter 3, I present a community-based case study currently under my coordination around Morro do Diabo State Park. The results of this experience show that only through the integration of applied research, involvement of NGO and Universities, co-management of protected areas, participation of local communities through community-based landscape restoration programs, environmental education and good policies will the jaguar have a chance to survive in this human dominated landscape

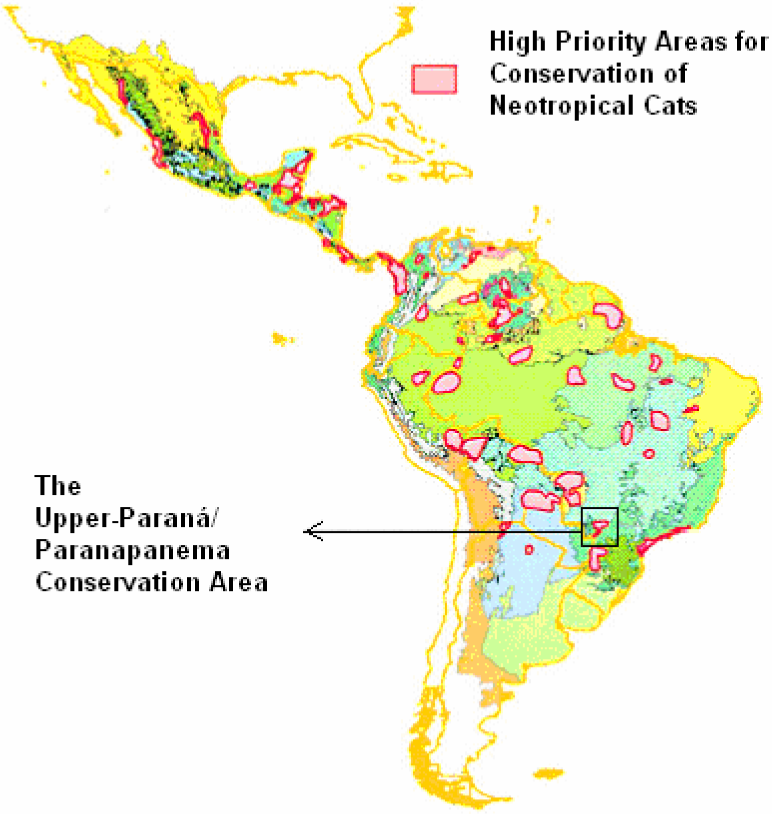

Figure 1.1. Jaguar conservation units (JCU) as suggested by Sanderson et al. (2002).

Chapter 4 aims to verify camera trapping density estimates of jaguar with radio telemetry. If species abundance can be demonstrated to be a useful indicator of habitat quality, then considerable attention needs to be directed toward the development of suitable techniques for estimating densities. Also, density and initial abundances are major variables in determining the spatial structure of the jaguar metapopulation, including location of suitable habitat patches and distances between them. This approach needs accurate density estimates to calculate demographic parameters (such as carrying capacities, density-dependent dispersal, dispersal rates and initial abundances) of populations, based on a user-defined function on habitat suitability in the patch. In addition, linked with population viability analysis (PVA) the landscape approach uses stage matrix models (Leslie 1945, Akçakaya 2002) to make projections of population's size and needs density information to specify the initial number of individuals in each age class. I then estimated jaguar density for the Morro do Diabo State Park, derived from both camera trapping and radio tracking methodologies. This is one of the first population estimates of a large carnivore where both methods were implemented simultaneously. The aims of this chapter were to estimate jaguar density in the study site using capture-recapture sampling approach with camera trapping data, to estimate jaguar density in the study site using VHF and GPS telemetry data, to compare both estimates, to provide information for the landscape detective approach and assess the implications for future jaguar population estimates and for conservation planning.

Chapter 5 aims to determine home range and movements of jaguars in the study region. In the landscape detective approach the link between the habitat suitability map and the metapopulation viability analyses is characterized by two parameters: *Threshold habitat suitability* and *Neighbourhood distance*. The *Threshold habitat suitability* is the minimum habitat suitability value below which the habitat is not suitable for reproduction and/or survival of the species. Based on field evidence and jaguar home range locations within the study region, a habitat suitability threshold value is determined for analysis. The *Neighbourhood distance* is used to identify nearby GIS grid cells that belong to the same patch or subpopulation, and may represent, for example, the mean foraging distance of the species or the size of the home range. I then used data from VHF and GPS radio tagged jaguars to quantify jaguar home range and movements and to incorporate this information in the landscape detective tool. I also investigate how home ranges vary seasonally and how home range size relates to habitat/prey parameters. I also analyzed jaguar's home range in the Upper Paraná River in comparison to other existing jaguar studies in the Neotropics.

The central point of the landscape detective approach is the animal's association with its environment, which includes habitat selection, and preferences of the animal. To understand habitat selection one needs to consider the influence of habitat availability. Habitat selection is the animal's answer to a great number of interdependent variables that make up the animal's environment. In the approach, a habitat suitability (HS) function is needed to identifying high suitable habitat patches for jaguars and the metapopulation scenario. At the same time, the habitat suitability acts as a bridge between the landscape data and the metapopulation model.

In Chapter 6, I used data from VHF and GPS radio-tagged jaguars to quantify jaguar habitat selection and how adult individuals in the Upper Paraná River region selected among the available habitat types. Habitat selectivity was defined by comparing availability and utilization using Ivlev's (1961) index of selectivity. I followed the framework developed by Johnson (1980) and Aebischer et al. (1993), in which animals make decisions about resource use at hierarchical stages, namely selection of home range within a study area (second-order selection) and selection of patches within a home range (third-order selection). I quantified habitat preferences at two orders of selection with respect to vegetation types and to test the null hypothesis that habitat utilization by jaguars was random at both study sites.

In Chapter 7, I consolidate the information from the previous chapters to develop and provide the data needed for the landscape detective approach. I provide a map and a habitat suitability model for the Upper Paraná Region that identifies important areas for jaguar conservation. I then link this model to a jaguar metapopulation scenario for viability analysis of the species and analyze the sensitivity of the viability of this species to different protection scenarios in model parameters.

In Chapter 8, I draw major conclusions of this study and make recommendations for the species conservation in the Upper Paraná region. It is my hope that these results will contribute to future state and national government efforts and well-founded conservation policies in the Upper Paraná region, and provide the basis for long-term landscape conservation planning within the Upper Paraná region.

CHAPTER 2

STUDY SITES

2.1 Atlantic Forest: A Global Ecoregion and a Hot Spot

Ecoregions are generically defined as large areas of relatively uniform climate that can harbour a characteristic set of species and ecological communities (Bailey 1998). WWF's Global Ecoregions Program is the first comparative analysis of terrestrial biodiversity to cover every major habitat type, spanning five continents that was developed by WWF scientists in collaboration with regional experts around the world (Olson et al. 2001). There is now a lot of interest in establishing a comprehensive network of marine ecosystems for the purpose of monitoring and protection. Marine protected areas are needed for the same reason that terrestrial ones are: to conserve the diversity of plants and animals within them. Part of WWF's program is to complete a network of marine ecosystems, in addition to terrestrial ecosystems, by 2010.

As used by WWF, ecoregions focus on large, biologically distinct areas of land and water, and set the stage for conserving biodiversity as a science-based global ranking of the Earth's most biologically outstanding terrestrial habitats. Ecoregion also provide a critical blueprint for biodiversity conservation at a global scale, ensuring that the full range of ecosystems is represented within regional conservation and development strategies (Grooves 2003). The Atlantic Forest in Brazil is among the 867 defined terrestrial ecoregions and is made up of the following terrestrial sub-ecoregions: Ilha Grande mangroves, Rio São Francisco mangroves, Araucaria moist forests, Rio Piranhas mangroves, Bahia mangroves, Pernambuco coastal forests, Bahia coastal forests, Bahia interior forests, Caatinga Enclaves moist forests, Pernambuco interior forests, Campos Rupestres montane savanna, Serra do Mar coastal forests, and the São Paulo-Paraná interior forests. This thesis was conducted within the sub-ecoregion of the São Paulo-Paraná interior forests.

The Atlantic Forest is also considered a “hotspot” for biodiversity conservation. A paper by Norman Myers in 1988 first identified ten tropical forest “hotspots” characterized both by exceptional levels of plant endemism and by serious levels of habitat loss. In 1990 Myers added a further eight hotspots, including four Mediterranean-type ecosystems. Conservation International adopted Myers' hotspots as its institutional blueprint in 1989, and in 1996, the organization made the decision to undertake a reassessment of the hotspots concept, including an examination of whether key areas had been overlooked. Three years later an extensive global review was undertaken, which introduced quantitative thresholds for the designation of biodiversity hotspots. To qualify as a hotspot, a region must meet two strict criteria: it must contain at least 1,500 species of vascular plants (> 0.5 % of the world's total) as endemics, and it has to have lost at least 70 % of its original habitat. In the 1999 analysis, published in the book *Hotspots: Earth's Biologically Richest and Most Endangered Terrestrial Ecoregions*, and a year later in the scientific journal *Nature* (Myers et al. 2000), 25 biodiversity hotspots were identified. Collectively, these areas held as endemic species no less than 44 % of the world's plants and 35 percent of terrestrial vertebrates in an area that formerly covered only 11.8 % of the planet's land surface. Furthermore, the habitat extent of this land area had been reduced by 87.8 % of its original extent, such that this wealth of biodiversity was restricted to only 1.4 % of Earth's land surface.

2.2 The São Paulo-Paraná Interior Forests: Biological Importance

The Atlantic Forest is one of the most threatened rain forests in the world (Galindo e Câmara 2003). Once covering approximately 1 million km^2 in Brazil, Paraguay and Argentina, only 7% of it currently remains scattered in fragments (SOS Mata Atlântica 2005). The Atlantic Forest is also known for its high endemism. More than 52 percent of the tree species and 92 percent of the amphibians in the Atlantic Forest are found nowhere else in the world (Jacobsen 2003). Many of these species, including 22 primate species and at least 158 species of birds, are critically endangered, because the vast majority of the Atlantic Forest has disappeared, (Ferraz et al. 2003).

A tri-national forest corridor lies within the São Paulo-Paraná interior forests, and pivots on the Argentine province of Missiones and eastern Paraguay, and includes Iguaçu National Park and other important protected areas and smaller forest fragments in Brazil (Di Bitetti et al. 2003) (Figure 2.1). This is the largest remaining area of the Interior Atlantic Forest sub-ecoregion and is on of the last refuges for jaguar in the Atlantic Forest Ecoregion (Sanderson et al. 2002).

Today, only about 58.000 km^2 remains of the Interior Atlantic Forest Ecoregion. Deforestation of this region has been most severe in Brazil where as little as 2% of the forests remains, and virtually none outside protected areas. About 22.000 km^2 of Sao-Paulo-Paraná Interior Atlantic Forest remains in Brazil, and 12.000 km^2 in Argentina, forming a contiguous corridor covering a large part of the province of Missiones (Di Bitetti et. al. 2003). Although Paraguay retains a larger area (24.000 km^2) of Interior Atlantic Forest than either Brazil or Argentina, deforestation in Paraguay has occurred in recent years at the highest rate of any country in Latin America and has fragmented the remaining forest (Altstatt et al. 2003). Conservation of the Atlantic Forest in this tri-national region is also important for the conservation of the biodiversity of the Upper Paraná River area.

2.3 Socio-Economic Context and Threats to the Region

In Brazil, the Atlantic Forest was the first area to be colonized and has developed into the agricultural, industrial and population centre of the country. The original Atlantic Forest cover has been reduced by centuries of unsustainable use into small forest islands surrounded by agricultural and urban development. In addition to containing “genetic banks” of some of the world’s rarest species, what remains of the Atlantic Forest is important for the quality of life of 70% of the Brazilian human population who live in the Atlantic Forest within 100 km of the coast. The remaining Atlantic Forest fragments are vital to watershed protection, prevention of soil erosion and siltation, and in maintaining microclimates and other environmental conditions necessary for the very existence of Brazil’s most populated cities and rural areas.

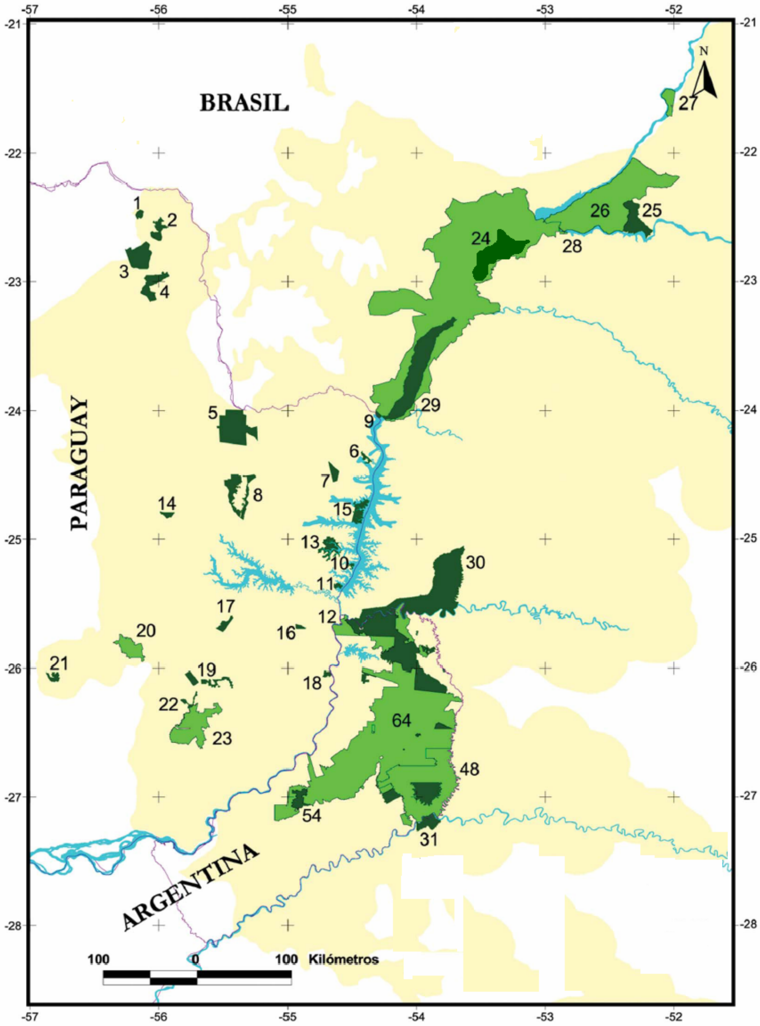

Figure 2.1. Some important protected areas along the Upper and the Lower Paraná River Ecoregion. Morro do Diabo State Park (25), Ivinhema State Park (24), Ilha Grande National Park (29) and Iguaçu National Park in Brazil and Argentina (30)(Source: Di Bitetti et. al. 2003).

However, the Atlantic Forest has remained isolated from human population centres in Brazil, Argentina and until recently in Paraguay. This has allowed the preservation of one of a large forest corridor. Nevertheless, only about 3% of the entire Atlantic Forest now occurs in protected areas. Many of these areas are not effectively protected, and their land tenure is unresolved (Furlan 2002). Existing protected areas are threatened in all three countries by the establishment of land reform settlements that use ecologically and economically unsustainable land-use practices within their boundaries or in adjacent areas (Cullen et al. 2005). Brush and forest fires, road construction, cutting of timber and firewood, agricultural expansion, uncontrolled tourism and urban sprawl are important threats to the

Atlantic Forest. In addition to deforestation, dams threaten the biodiversity of the Upper Paraná River Ecoregion (Holz and Placi 2003).

2.4 The Land Reform and Biodiversity Conservation

Pontal do Paranapanema Site: Some of the largest forest remnants of the Upper Paraná Atlantic Rainforest Ecoregion lie in the Pontal do Paranapanema area of western São Paulo state were originally designated a public forest reserve and were progressively encroached upon between 1960-1990 by large scale ranching and sugarcane establishments. In the mid-1990s, with pressure for land redistribution from the Landless Rural Workers' Movement (MST) and other groups, many such properties were first occupied by MST affiliates. These lands were later expropriated for public land reform settlements, dramatically increasing the density of human occupation. Their tenure is insecure, since large landowners did not subsequently encroach on remaining forests, seeking to negotiate permanence. After settlement of more than 5.000 landless families, the pace of land redistribution consequently slowed, and policies adopted at a national level sought to consolidate existing settlements. There is an urgent need to promote the protection of the remaining fragmented biodiversity within this productive landscape before further pressures ensue. The non-profit organization Instituto de Pesquisas Ecológicas (Institute for Ecological Research - IPÊ) has studied the forests in Pontal do Paranapanema and has undertaken conservation initiatives, such as environmental education, community involvement, habitat restoration and the promotion of policies that protect natural areas while simultaneously empowering people to improve their conditions of living. For 15 years IPÊ has been engaging with the regional stakeholders to secure the conservation and the recovery of forests in the Pontal do Paranapanema Area (Valladares-Padua et al. 2002, Cullen et al. 2001, 2005).

The Upper Paraná River: This region strategically connects the Morro do Diabo State Park to other large protected areas along the Paraná River, including the Iguaçu National Park in Brazil and Argentina. These core areas (Figure 2.1) form the basis of the Upper Paraná Atlantic Rainforest Biodiversity Vision, a large scale landscape conservation plan developed by WWF. In this region approximately 160 Agrarian Reform Settlements have been created during the last 20 years. World Wildlife Fund (WWF-Brazil) efforts are focused on the implementation of the Iguaçu National Park as a World Natural Heritage Site, the creation of the RPPN (Private Reserve of Natural Heritage) "Corredor do Iguaçu" and the establishment of an environmentally sustainable "Celso Furtado Agrarian Reform Settlement" which is in the process of being created by the Brazilian Government after 7 years of negotiations with the Landless Rural Worker' Movement (MST). The "Celso Furtado Settlement" will be home to about 1.000 families. This settlement is located in a very sensitive landscape with the last remnant of rare transitional Atlantic Rainforest between the semi-deciduous forest and the Araucaria forest. Poverty is big issue and WWF-Brazil has been building a participatory project that can secure both family livelihood and the protection of these forest remnants since 2003.

2.5 The Study Sites within the Upper Paraná Atlantic Forest

The Upper Paraná Atlantic Forest is an appropriate landscape to test and apply the landscape detective approach with the jaguar. The ongoing destruction of the Atlantic forests are confining remaining jaguar populations into networks of small patches of suitable habitat. Thus, a reliable method of determining the requirements for effective landscape biodiversity conservation needs to be developed that includes metapopulations and persistence of key species. Using the jaguar as the landscape detective species, the research presented in this thesis seeks to develop and implement a spatially realistic metapopulation model, which includes the effects of patch area and isolation on extinction and colonization. This modelling approach also seems to provide a practical tool in the design of a nature protected area network in this tri-national forest corridor and should and should also be used with other species in this highly fragmented landscape.

The jaguar workshop "*Jaguars of the New Millennium*" (Sanderson et al. 2002) held in Mexico in 1999 was an important starting point to identify critical areas for jaguar conservation (*Jaguar Conservation Units – JCU's*). Two of the areas identified as important Jaguar Conservation Units are JCU 250 (The Upper Paraná River) and JCU 257 (Missiones – Argentina, Brazil). These two JCU's are located in the tri-national area spanning the borders of Argentina, Brazil and Paraguay, and comprise an area of approximately 50,000 km^2 (Figure 2.2). These areas are considered important for research and conservation efforts on jaguar populations due to their long term conservation prospects and ecological peculiarities. Jaguars are also considered keystone species for the Brazilian Atlantic Forest and, in these specific jaguar conservation units, have been selected as a keystone and umbrella species for the development of conservation plans according to the World Wildlife Fund "Biodiversity Vision" (Di Bitetti et al. 2003).

Moreover, this study involved endangered jaguar sub-populations of two protected areas along the "Green Corridor" in the Brazilian Paraná River Basin, the Morro do Diabo State Park (MDSP), 370 km^2, and Ivinhema State Park (ISP), 720 km^2. Both protected areas are surrounded by a mosaic of agriculture, extensive cattle ranching, agrarian settlements, forests and marshlands, and provide a unique opportunity to study and conserve jaguars. These two protected areas, are partially connected by well-preserved patches of semidecidual Atlantic forest and marshlands. They are considered among the few areas where large carnivores such as jaguars, pumas and ocelots might persist in the long-term, if well managed (Sanderson et al. 2002; Figure 2.1). Other similar protected areas, although located in the lower parts of the Paraná River are the Ilha Grande National Park (740 km^2, Brazil), Iguaçu National Park side in Brazil (1750 km^2, Brazil, Iguaçu Park side in Argentina (550 km^2), the Urugua-í Private Wildlife Reserve (34 km^2, Argentina) and the Urugua-í Provincial Park (840 km^2, Argentina).

2.6 The Morro do Diabo State Park

The Morro do Diabo State Park lies within the northern part of the Green Corridor and is located in the Pontal do Paranapanema, a wedge-shaped region bounded on the north by the Rio Paraná and on the south by the Rio Paranapanema, forming the westernmost extremity of the State of São Paulo (22° 30' S, 52° 20'

W). Entirely forested, the region was decreed a protected area in 1942 by the state of São Paulo, the “Grande Reserva do Pontal”, with 2600 km^2 ha (Leite 1998). Despite the protected status, the Pontal has suffered from numerous conflicts over land ownership, resulting in the widespread destruction of its forests for timber and cattle pasture during the past 50 years.

Today all that remains of the “Grande Reserva” is the 370 km^2 Morro do Diabo State Park. The Morro do Diabo State Park is well protected with legally demarcated, nondisputed boundaries. It is the last significant remnant of Atlantic forest in the west of São Paulo state, where only 1.8% of the original natural vegetation remains (Figure 2.3). Because of this extensive loss of forest, the conservation of the Morro do Diabo State Park and other widely scattered, smaller, forest remnants is of utmost importance, as they still harbour the rich and endemic biodiversity of the region, and many of its endangered species, such as the jaguar

The forests of Morro do Diabo are considered a transitional ecosystem, bordered by tropical evergreen broadleaf forest to the east, which originally covered the Atlantic coastline, and the dry cerrado vegetation to the north and west (Ab'Saber 1977). Cerrado comprises a tall dense semideciduous xeromorphic savanna vegetation (Baitello et al. 1988). The Pontal region is characterized by a pronounced dry season with annual precipitation averaging 1,370 mm, of which about 30% falls between April and September (Valladares-Padua 1987, 1993). Most of the emergent trees lose their leaves during the dry months (Hueck 1972). The region is also known for its generally nutrient-poor sand soils (Setzer 1949).

Important prey species for jaguars found in the Morro do Diabo comprise tapirs (*Tapirus terrestris)*, white-lipped peccaries (*Tayassu pecari)*, collared peccaries (*Tayassu tajacu)*, capybaras (*Hydrochaeris hydrochaeris*), armadillos (*Dasypus novencintus* and *Euphractus sexcintus*), giant anteaters (*Myrmecophaga tridactyla*), raccoons (*Procyon cancrivorous*), brocket deer (*Mazama* sp.), azara's agouti (*Dasyprocta azarae*), and South American coati (*Nasua nasua*). Pumas (*Puma concolor*), ocelots (*Leopardus pardalis*), margays (*Leopardus weidi*), crab-eating foxes (*Cerdocyon thous*), howler monkeys (*Alouatta fusca*), capuchin monkeys (*Cebus apella*), and the critically endangered black lion tamarins (*Leontopithecus chrysopygus*) also inhabit the Morro do Diabo State Park and some of the surrounding forest fragments.

Figure 2.2. Distribution of Jaguar Conservation Units (JCUs) in Latin America. The black box shows two areas identified as important Jaguar Conservation Units included in this study. Above, the JCU 250 (The Upper Paraná River) and below, JCU 257 (Missiones – Argentina, Brazil). These two JCU's are located in a tri-national area spanning the borders of Argentina, Brazil and Paraguay. (Source: Sanderson et al. 2002)

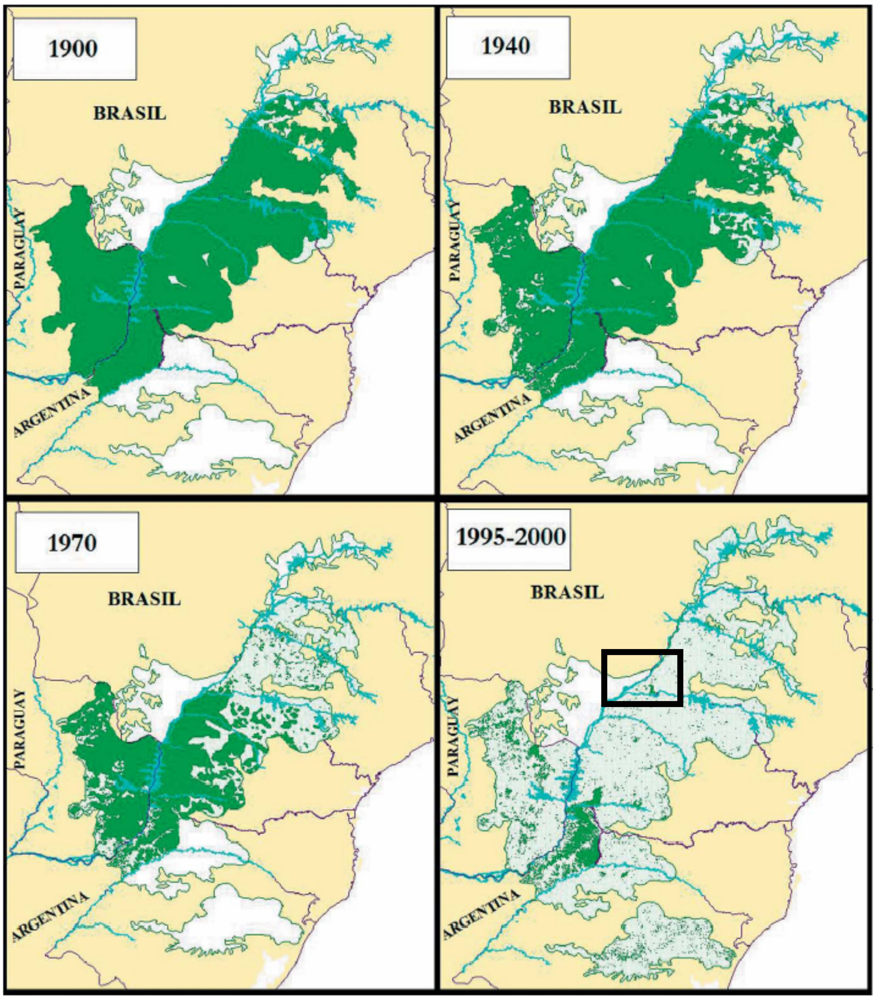

Figure 2.3. The forest fragmentation process along the Paraná River Basin. The black box in the final panel shows the Pontal do Paranapanema Region and in the centre the Morro do Diabo State Park (Source: Di Bitetti et al. 2003).

2.7 The Ivinhema State Park

The Ivinhema State Park, in the northern part of the Upper Paraná River, was formally established in 1998 as a compensation measure for the damming impacts o São Paulo Energy Company (CESP) in the Upper Paraná River. Ivinhema is 720 km^2, and is located 150 km southwest of Morro do Diabo forest in the south-eastern corner of the State of Mato Grosso do Sul and comprises several former cattle ranches. The eastern boundary of Ivinhema is formed by the Paraná and the Ivinhema rivers. Smaller streams also run through the area and the lowest elevation is approximately 150 m above sea level, in the open savannas in the southern part of the Ivinhema. The landscape can be characterized as a complex mosaic of interdigitated forest patches and open areas, with vegetation types based on the interaction of elevation, substrate, hydrology and past perturbations, such as logging and fire. The main habitat types in Ivinhema are seasonally flooded savannas (dense and open marshes), seasonally flooded semi-deciduous forests (alluvial forests), dry hillside savannas, dry hillsides cerrados, dry semi-deciduous forests, gallery forests, and abandoned pastures with some illegal livestock maintenance.

The climate is markedly seasonal, and most of the 1.450 mm of the yearly precipitation falls between early October and late March. The dry season extends from April to September. Relatively impermeable soils in some areas of Ivinhema causes surface water to accumulate from November. The inundation by the Ivinhema and the Paraná rivers is relatively shallow, with the greatest depths occurring in the low savannas in the southern portion of Ivinhema. Forests typically retain some dry land, whereas the savannas in the south and the alluvial areas in the north remain flooded for several months. Important prey species for jaguars found within the park are tapirs, both species of peccaries, capybaras, marsh deer (*Blastocerus dichotomus*) and caimans (*Caiman latirostris*). Pumas, ocelots, crab-eating foxes, howler monkeys (*Alouatta caraya)* and capuchin monkeys (*Cebus apella*) are also found in Ivinhema and in some of the surrounding forest fragments.

CHAPTER 3 [1]

LAND REFORM AND CONSERVATION IN THE ATLANTIC FORESTS

3.1 Introduction

The survival of jaguars and other species in highly fragmented, rural landscapes will depend on finding ways to integrate people, wildlife and protected areas. The land reform and environmental movements, revitalized by the democratization of civil society in Brazil in the 1990s, found themselves in conflict with the conservation of biodiversity. To integrate land reform and biodiversity conservation in the Atlantic Forests the following should be accomplished: 1) reduce deforestation and biodiversity loss and increase rehabilitation of forest and forest habitats, 2) contribute to poverty alleviation and an improved quality of life for the land reform settlers and, 3) promote the conservation and sustainable management in key areas identified by the landscape detective approach. In the Atlantic Forest, where 95% of the forest is gone, three cases are reviewed of Brazilian NGO engagement with the land reform movement with respect to forest remnants neighbouring protected areas that have insufficient habitat for the long term survival of unique endangered species such as the jaguar. The construction of landscapes with both forest stewardship and poverty-reducing agrarian reform faces continued obstacles, according to these cases, from contradictory agrarian and environmental sector policies and inadequate economic incentives for forest stewardship on private lands.

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[1] **This chapter is based on the following published articles:**

Cullen, L. Alger, K., and Rambaldi, D. 2005. Land Reform and Biodiversity Conservation in Brazil in the 1990s: Conflict and the Articulation of Mutual Interests. *Conservation Biology* **19**: 1-9.

Cullen, L. Ferreira-Lima, J. and Pavan, T. 2004. Agroforestry buffer zones and stepping stones: tools for the conservation of fragmented landcapes in the Brazilian Atlantic Forest. In: *Agroforestry and Biodiversity Conservation in Tropical Landscapes*. Eds: Schroth, G., Fonseca, G. A. B., Harvey, C. A., Gascon, G., Vasconcelos, H. L. and Izac, A.M.N. Pp. 415-430. Island Press.

Many independent agrarian reform organizations and conservation NGOs were born, revived and greatly strengthened, when the Brazilian military government ended in 1984. Their common cause was rooted in two decades of environmentally-destructive megaprojects, such as government-sponsored colonization of the Amazon and industrial expansion fired by charcoal from the dwindling Atlantic Forest. In both the Amazon and the Atlantic Forest, the principal cause of rapid deforestation was government policies, and the principle beneficiaries were owners of large rural estates (Dean 1997, Evans 1979 Fearnside 1993). In the 1990s, large cattle farms in São Paulo, which had been carved out of state forest reserves in the 1950s, began to be occupied by landless rural workers, led primarily by the Movement of Rural Landless Workers (*Movimento dos Trabalhadores Rurais Sem Terra,* or MST). This resonated across Brazilian society as social justice, as it followed the death of Chico Mendes, labor leader of Amazonian rubber tappers, killed by cattle ranchers in 1988 for defending the forest.

Poor land-stewardship on the part of farmers became a unifying theme for both the land reform movement and Brazil's rapidly expanding environmental movement. Despite this, rampant rural poverty and the lack of government determination to address agrarian reform rapidly drove a wedge between them. Rural workers increasingly occupied unused lands when the government failed to implement land reform according to the provisions of the 1988 Constitution (Teófilo and Garcia 2003). Judicial decisions after occupation often favoured nominal titleholder rights, but police were frequently unable or unwilling to evict the occupants. Landowner-organized vigilante attacks upon occupiers commonly followed, and the escalation of rural violence motivated judicial decisions revoking titleholder claims (Heredia et al. 2003, Medeiros and Leite 1999). Only then did governmental land reform agencies, led by the National Institute for Colonization and Agrarian Reform (INCRA), begin intervening. Disputes were resolved extra-judicially, with INCRA providing the justification for appropriation, indemnification, and official recognition of land reform settlements as eligible for government assistance. Ninety-five percent of land reform settlements in a sample of those originating between 1986 and 1997 began with land tenure contestation rather than through government initiatives (Heredia et al. 2003).

The landless movement, however, lacked the political “weapons”[1] to claim the more valuable agricultural land. Brazil’s agrarian reform law, outlined in its 1964 “Estatuto da Terra” (Law 4504, Article 1, Paragraph 1), also called for “a better distribution of land […] through appropriation and indemnification of *unproductive* properties and their distribution to rural workers” (my italics). INCRA interpreted this to mean that properties having more than their legally required 20% Forest Reserve were unproductive (Dean 1997). Extensive uncultivated land on a property was presented before courts as cause for the suspension of a titleholder claim[2]. Marginal lands were also less likely to be violently defended, as they tended to have soils and topography poorly suited for agriculture. Of the land appropriated by INCRA between 1997 and 1999, only 21.1% was in agricultural use before occupation (Teófilo and Garcia 2003). The land reform settlement-clusters within the Atlantic Forest states tended to be in municipalities with more forest remnants than average (SOS Mata Atlântica and INPE 2002).

Contradictions between land use for agrarian reform and for conservation remained largely unnoticed (Viola 1991). Activists attributed deforestation in the Atlantic Forest to inadequate enforcement of forestry laws, residential expansion, and commercial agriculture (Young 2003).

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[1] Peluso (1992, p.13), building on the work of Scott (1985) argues that the “repertoire of resistance” is a product of “specific historical and environmental circumstances. The forms that resistance takes depend on the nature and generality of the complaint and the kinds of ‘weapons’ (social, political, or broadly defined technological) at the disposal of the resistors”.

[2] Landownership requires productive use in terms of the lands’ economic, social and environmental functions, according to the 1988 Constitution. While the extent of “unused” land was the legal wedge used by MST in the early 1990s, by the end of the decade, MST argued that deficient social functions of lands employed in monocrop, input-intensive agriculture should also legally disqualify titleholders from land tenure.

Media coverage of rural land struggles emphasized their social aspects, while urban environmentalists had more immediate concern for urban pollution, congestion, and nuclear power plants. Nonetheless, the environmental aspects of land reform settlements began to be addressed through pilot projects under the National Environment Fund (Brazil, FNMA 2001), promoting agricultural practices that diminished deforestation and fostered livelihoods. Some environmental groups, however, began questioning whether rural poverty could be solved within the confines of land reform settlements on the remaining 5% of forested land in the Atlantic Forest, particularly because the previous conversion of 95% of the land to agriculture had not solved the problem. The progressive degradation of lands occupied for agrarian reform triggered a regulatory ruling by Brazil's National Environment Council (Resolution 289, October 25, 2001; Brazil, CONAMA 2001) requiring prior environmental licensing of areas under consideration for agrarian reform settlements.

Although critiques of the environmental impacts of settlements mounted (Graziano 2003), there were also concrete examples of collaboration between environmental and land reform groups. Some conservation NGOs broadened their focus from the front-line defence of existing protected areas to a regional, landscape planning perspective that considered multiple land use options, including the integration of private reserves and other conservation measures with agrarian reform settlements. The organized land reform groups have also increasingly taken on technical assistance to orient land use on settlements, respecting environmental objectives, and have sought to establish means to legally challenge land title independent of the extent of uncultivated land (MST 1999). Here I highlight three cases where local environmental groups have engaged with the land reform movement on technical issues involving the conservation of threatened species in the Atlantic Forest.

3.2 Landlessness and Conservation in the Pontal do Paranapanema

In 1942, there was a large forest reserve, the "Grande Reserva do Pontal" of 2468 km^2, covering most of the westernmost part of the state of São Paulo - the "Pontal do Paranapanema" (Ferrari Leite 1998). Dean (1997) recounted the extraordinary history of the occupation of the region and, despite its protected status, the forests were largely destroyed during the 1950s and 1960s. The existence of the forest reserve, however, has meant that the titles to the vast ranches that exist there today are contestable - a reason why the MST has been particularly active in the region. Besides scattered fragments, only the 360 km^2 Morro do Diabo State Park remains, the stronghold of the black lion tamarin (*Leontopithecus chrysopygus*) and the jaguar (*Panthera onca*) now the flagships species for the region, and otherwise practically extinct throughout their original range in the state. A second reserve, the federally-administered Mico-Leão-Preto Ecological Station, was created nearby, in July 2002, as a result of the research and actions of a local NGO, IPÊ – Instituto de Pesquisas Ecológicas. It covers the four largest remaining forest fragments, with a combined area of 62 km^2. Other scattered forest fragments add up to a further 70 km^2, mostly privately owned or in agrarian reform settlements. The Pontal is also home to ocelots, pumas, tapirs, white-lipped peccaries, king vultures and the blue-and-yellow macaw. Metapopulations of these species are still considered viable mainly due to the Morro do Diabo State Park, but also to the fact that the larger fragments still contain most of the original biota (Cullen et al. 2002). The forest remnants also serve as the last remaining seed sources for forest restoration programs.

3.3 Agrarian Reform and Conservation of Biodiversity

Deforestation in the Pontal from 1987-2001 occurred at a rate of 1.5% a year. At that rate, 34% of the remaining forest would be lost over the next three decades (probably an underestimate as it does not include recent settlers). The forest patches within agrarian reform settlements will also be degraded through edge effects. As a result of this diagnosis, IPÊ began to work with settlers as well as the owners of the larger properties. While posing enormous challenges to conservation, the settlements also present opportunities for innovative approaches, and community leaders in land reform settlements have taken an interest in agroforestry and landscape planning, combining small-scale agriculture and conservation.

For 15 years IPÊ has been engaging with the regional stakeholders to secure the conservation and the recovery of forests in the Pontal (Padua et al. 2001). Landscape planning at a regional scale is possible when local communities are involved, and barriers to the adoption of alternative agroforestry practices arise from a lack of farming expertise - training is a vital component of the programme although also important is the capacity to navigate government policies and credit practices to ensure effective support. Gaining the confidence of the local communities in sharing in technical collaboration in agricultural practices and environmental education has allowed for collaborative planning of priority areas for wildlife corridors that allow demographic interchange between isolated habitats. Where corridor creation is impractical, stepping-stone and agroforestry buffer habitat is planned around biologically vital areas, such as the Morro do Diabo State Park.

The technical training provided by IPÊ is intended to create incentives and remove barriers to the adoption of agroforestry systems. Community members learn to manage tree nurseries, identify and demarcate seed bearing trees, plan seed collection programmes, and conserve and restore seed viability. The nurseries contribute seedlings to establish forest corridors and buffer zones around the forest fragments. Support for producer groups, who collectively seek training and financial support for certification and value-added enterprise development (e.g., shade grown coffee), is vital, as is the identification of credit sources. Training is also important to protected area managers for effective management of Morro do Diabo within the context of its surrounding landscapes and communities. Wildlife management plans, for example, need to consider both protected areas and surrounding buffer areas, especially for large cats and ungulates. Research on wildlife ranging and dispersal requires collaboration among settlers, NGOs, and park managers.

IPÊ's work has also demonstrated that viable landscapes can be rebuilt from small fragments through regional planning and with strong and broad support among the landholders. In 2003, the principal decision-makers in the Pontal region responsible for land use planning adopted priorities shown on a map produced by IPÊ (Figure 3.1) as a regional development guide. It identifies areas for potential forest corridors on land reform settlements that can be designated as their collective and obligatory forest reserve. Planning for connectivity on land reform settlements is simpler than among private property owners due to the public character of lands assigned provisionally to them.

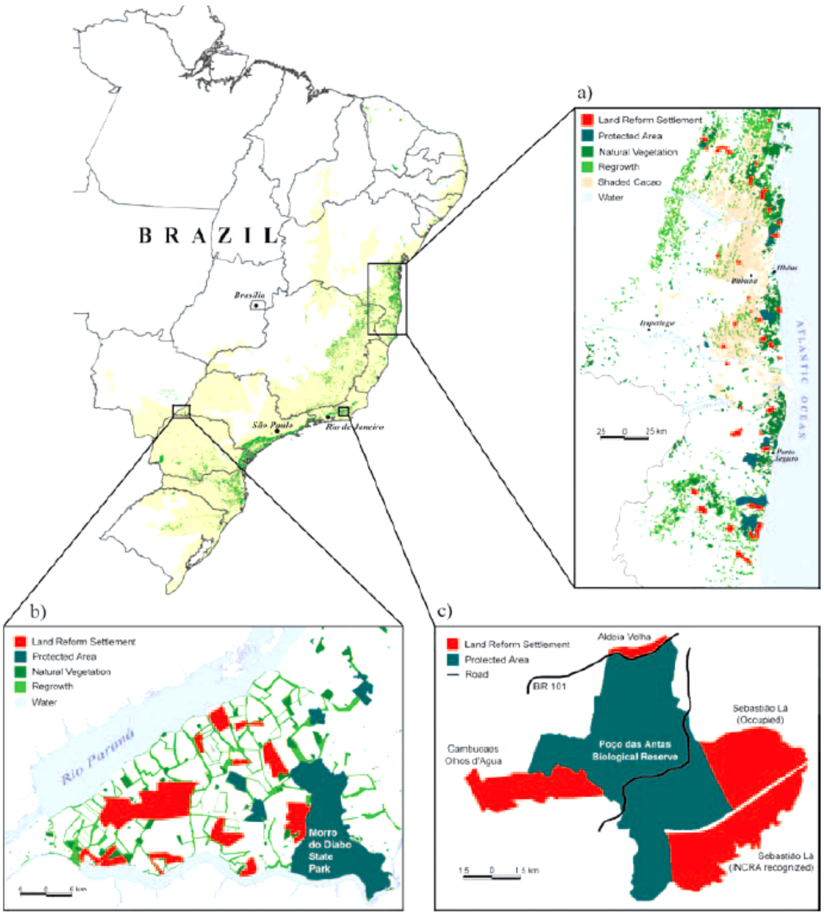


Figure 3.1. The original (yellow) and the current (green) extents of the Atlantic Forest with insets showing land reform settlements and protected areas in (a) Southern Bahia, (b) Pontal do Paranapanema and (c) Poço das Antas.

The programme sponsors forums twice a year to facilitate dialogue among stakeholders, to discuss the regional plan and the progress in its implementation. Settlers meet with representatives of the key public agencies responsible for land use management to discuss emerging issues and organize joint activities to resolve or reduce socio-environmental conflict. A parallel effort has been undertaken to develop practical approaches and policing capacity to implement the regional land use plan. Landowners, the public prosecutor, and environmental agencies have been brought together to coordinate efforts towards the demarcation of forest reserves and reforestation areas, as well as to enforce the maintenance of Areas of Permanent Protection (*Áreas de Proteção Permanente*), such as gallery forests and forests on steep slopes, as required by law.

3.4 Land Reform and Conservation Around the Poço das Antas Biological Reserve

The Poço das Antas Biological Reserve was created in 1974 in the state of Rio de Janeiro to protect another of the Atlantic Forest's flagship and highly threatened primates, the golden lion tamarin (*Leontopithecus rosalia*). When created, it was the only protected area for the species, and remaining forest fragments elsewhere were so small and isolated that a captive breeding and reintroduction program was set up to avoid its extinction in the wild (Kleiman and Rylands 2002). After 21 years of intensive conservation efforts, the wild population is recovering, but is still below the goal of a minimum viable population of 2.000, an objective set for 2025 (Seal et al. 1990). Species viability studies have shown that at least 250 km^2 of lowland forests are required for its long-term survival. Only 2% of the forests in its original range are still standing (Kierulff and Oliveira 1996), and every remnant has to be considered vital for reconstructing landscape connectivity and expanding forest cover.

Of the 98 km^2 appropriated by INCRA in the municipality of Casimiro de Abreu in 1974, 53 km^2 went to the biological reserve and the remainder was for agrarian reform. The first 900 ha settlement, Aldeia Velha, involved 91 families and borders the reserve to the north. Only a few dozen remain as many properties were subsequently sold to residents of neighbouring cities for second homes, and others were combined and became cattle ranches. The legal requirement for 20% of each property to be retained as a Forest Reserve was ignored, and the vegetation was largely destroyed on the steep hillsides and riverbanks. The settlement's social organization has always been precarious and unstable, and despite efforts in training and environmental education by the principal local NGO, the Golden Lion Tamarin Association (*Associação Mico-Leão-Dourado,* or AMLD), it remains largely unengaged and disinterested.

A second settlement created by INCRA in 1994 for 104 families was triggered by the occupation of a 1,200 ha property (Cambucães - Olhos d'Água). The existing legally-required Forest Reserve was divided up for 19 families, whose only option was to log it and cut it down. The Brazilian Institute for the Environment (IBAMA) later fined these families - a fruitless effort that only resulted in making them ineligible for access to subsidized credit. Another 21 families demanded, but did not receive land until 2001, when INCRA ruled for their indemnification and translocation to another, undetermined settlement project. INCRA ignored a 1990 resolution of the National Environment Council (CONAMA) requiring that impact assessments precede the expansion of any economic activity occurring within 10 kilometers of a federal protected area boundary.

Since 1998, AMLD has worked with the leaders and families of the Cambucães - Olhos d'Água settlement to promote sustainable agricultural practices, and has facilitated relations and negotiations between the community, IBAMA, INCRA, and the local municipalities. AMLD promoted the restoration of forested land on settler lots to compensate for the area deforested from the original forest reserve. AMLD also trains schoolteachers in environmental education, and in the management of "green fertilizers", agroforestry nurseries and test plots, the use of hedges (as an alternative to fences), and the reforestation of degraded areas with native tree species. Although the community's social organization underwent many changes over this period, its greater internal coherence facilitated interaction with the environmental groups. Similar to IPÊ's experience in the Pontal region, AMLD is working with the Cambucães - Olhos d'Água community, creating connectivity, re-establishing gallery forest corridors to allow for the dispersion of species.

Five hundred ha acquired for land reform by INCRA in 1974, but subsequently controlled by a single landholder claiming title, was invaded by MST organized settlers in 1997. Unfortunately, one of the settlers who was later expelled started up a fire which swept through and significantly damaged the Poço das Antas Biological Reserve. Since then, conservation groups, IBAMA, and the settler's leaders have collaborated on land-use planning, environmental education, and agriculture, drawing on the experience gained with the Cambucães - Olhos d'Água community. Thirty families were settled in the area after it was officially recognized by INCRA in 1999 for land reform. There was a delay in INCRA recognizing the legitimacy of a similar site with an encampment of 83 families organized by the MST, when IBAMA took out a civil action against INCRA, demanding that it conduct an environmental impact assessment required by CONAMA (Resolution No. 13, 1990). This revealed the inadequacy of the environmental assessment protocols, designed primarily for industrial projects, in evaluating land reform initiatives and resulted in a new CONAMA resolution (No. 289/2001) establishing a new protocol specifically for land reform settlements. The federal public prosecutor's office, recognizing the urgency of the situation for the encamped settlers and the threat to golden lion tamarins, ruled for the creation of a multidisciplinary evaluation team, coordinated by the Fluminense Federal University, with the participation of NGOs and other stakeholders. There are now high hopes that this process will lead to a compromise that addresses the needs on both sides.

3.5 Land Reform and Conservation in Southern Bahia

As in the Pontal de Paranapanema and the Poco das Antas areas, environmental NGOs in the Atlantic Forest of southern Bahia have increasingly sought common ground on technical issues with organizations promoting land reform settlements. As with IPÊ and AMLD, small environmental groups such as Gambá, Jupará, and the Instituto de Estudos Sócio-Ambientais do Sul da Bahia (IESB) have sponsored projects to train land reform communities in agroforestry, tree-crop nurseries, wildlife and water issues, and land-use planning. Southern Bahia is a cocoa-producing region, and its forests have generally not (yet) been reduced to the hard-edged fragments typical of the regions discussed above. Naturally shaded cacao plantations remain an important component of the landscape, connecting the forest fragments. With more forested remnants on private lands than in the Pontal, and with significant agroforestry still providing some landscape connectivity, environmental groups have focused on influencing public policy to avoid further fragmentation rather than on reconstructing connectivity.

Approximately 200,000 rural workers lost employment on cacao plantations in Bahia in the early 1990s as declining world prices could not cover producer costs amid an outbreak of the fungal witches' broom disease (Demeter 1996). While out-migration from the region was significant, unemployed rural workers constituted a reserve army of the poor for the organized land reform movement. Organizations of the land reform movement in Bahia were more heterogeneous than in the Pontal, where the MST was dominant. The human rights of rural settlers were first defended in Bahia by representatives of the Catholic Pastoral Commission of the Land (CPT): other groups have included labour organizations (CUT-Rural), the Land Liberation Movement (MSLT) and the Movement for the Struggle of the Landless (MLT). Land reform settlements in the 1990s tended to be established on properties with more forest remnants, induced by the technical and legal standards designating properties with above-minimum native vegetation as unproductive (Table 3.1). While land reform settlements have been an increasing source of pressure on forest remnants in Bahia, they contributed less to deforestation in the 1990s than that on lands controlled by large landowners (Alger 1998, Trevisan 2004).

Table 3.1. Land reform settlement location in Southern Bahia in relation to land use 1986-1990.

	Number	% Natural vegetation	% Agriculture/ Urban
South Bahia Municipalities in broadleaf evergreen tropical forest zone	109	22	74
Municipalities in South Bahia with land reform settlements 1986-2000	23	34	57
1986-2000 South Bahia Land Reform Settlements, including surrounding lands within 3 kilometres	38	42	52

Environmental NGOs sought to influence the locations chosen for land reform in southern Bahia by building awareness of existing public policy, such as the CONAMA resolution 13/1990 with use limits on areas within 10 km of the boundary of federal conservation units, and with regard to the habitats of threatened species. Despite these regulations, IBAMA had approved numerous logging concessions on private lands within 10 km of the Una Biological Reserve, where researchers confirmed the presence of two threatened primate species, the golden-headed lion tamarin (*Leontopithecus chysomelas*) and the yellow-breasted capuchin (*Cebus xanthosternos*). The federal public prosecutor's office was informed, and use restrictions were disseminated through maps showing the affected properties. NCRA and land reform community technicians were also apprised of these limitations, which effectively restrict the prospects for INCRA to appropriate land in favour of settlers, thereby undermining the incentive for organizers to occupy these lands in the first place.

Soil maps and independent studies revealing the poor agricultural suitability of coastal soils underlying most remaining forest fragments were shared in meetings with land reform activists. In specific cases, environmentalists helped the landless find more appropriate and already deforested agricultural land, enhancing shared interests. In one case, a 500 ha, completely forested, property (Fazenda Oregon) within an area to be designated by the state of Bahia for the Conduru State Park was occupied by settlers in 1997. Working with community leaders, IESB obtained support from the state forestry agency, INCRA, and the settler's representatives to relocate them to a bankrupt cacao farm in the neighbouring municipality of Uruçuca. NGO assistance for agricultural practices on this site continued.

The complexity of regulations was the subject of numerous meetings with cacao landowners seeking to understand legal liabilities when eliminating shade cacao in favour of annual crops, coffee and palm plantations. Common misunderstanding of regulations revealed how complexity and unclear authority among multiple enforcement agencies discredit government environmental policy in the eyes of farmers. While some knew about the 20% forest reserve requirement, few were aware that the law also required permanent protection of natural vegetation along streams and on steep slopes. While fewer than 7% of private lands in the region are forested, much more than 20% of the total area would need to be forested to meet minimum legal requirements in this region of steep slopes and abundant rivers and streams. Further confusion is caused by contradiction between state environmental regulations (Conselho Estadual de Meio Ambiente CEPRAM, Resolution 1157) permitting suppression of vegetation in abandoned cacao groves, and federal regulations requiring protection of vegetation in an "advanced state of regeneration."

MST's arrival as an organizing force in the region in 1997 was marked by occupation of agricultural areas on better soils, close to asphalt roads, rather than the more remote forested areas chosen early in the decade. MST, unlike other groups, was also more likely to employ agricultural technicians. Often these were agronomists trained at the same universities as the agronomists working for environmental groups, and could communicate on the issue of the agricultural suitability of soils and practices. During the 1990s, the land parcels occupied by settlers tended to be less forested and more agricultural, even though there continued to be occupations of forested parcels for conversion to agriculture (Figure 3.2).

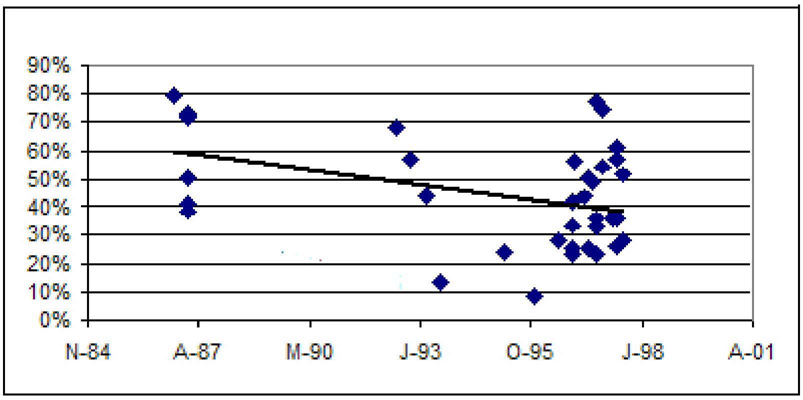


Figure 3.2. Natural vegetation within 3 km of land reform settlements in southern Bahia 1986-2000. (*y=2.2797-0.000045x; t = - 2.23,* R^2 *= 0.165).*

3.6 Conclusions

There has been considerable progress in improving mutual understanding between conservation NGOs and organizations of the landless in the past 10 years. Practical experience has allowed both to see that they did not face a zero-sum conflict over the same lands. Since agricultural suitability was minimal on land for conservation, land reform activists realized that these areas contributed little to poverty reduction. Conservation NGOs studying the socio-economy of the cacao industry also discovered that the economies of disease control and management would make shade cacao more viable with family labour on smaller plots than under the system of large plantations using wage labour.

Federal laws and regulations continue evolving to change incentives affecting forest conservation and land reform in Brazil. Federal regulations in 2001 (Medida Provisória 2166–67, 24 August 2001) permitted landowners to meet forest reserve requirements by compensating non-compliant reserves by acquisition of approved lands with natural vegetation, preferentially within the same watershed. The new rules mean that forest in excess of the minimum Legal Reserve on private lands may become viewed as “productive” and could counterbalance the current landholder incentives to deforest remnants to avoid being targeted for occupation and land reform (Chomitz et al. 2004). An unexpected benefit from this legislation was that it facilitated the creation of the 38670 Km^2 Mountains of Tumucumaque

National Park in Amapá in 2002. The designation of these lands was also compensation for non-compliance by INCRA with the Legal Forest Reserve requirements on their Amazonian land reform settlements. More recent land reform settlements in Amazonia are both the source of much illegal logging, and potentially the best positioned to work with NGOs in supplying the market with low-impact certified logging (Nepstad et al. 2004).

In the three cases reviewed here, environmental NGOs found that where land reform settlements had better internal organization, there were more opportunities to ameliorate environmental impact, work towards sustainability on the settlements, and plan together to find landscape elements providing connectivity for threatened species. The NGOs also found that site-scale confidence building was necessary to reach a landscape scale of engagement. To avoid species extinction, all the NGOs realized that broader-scale work is the only technically viable approach, though all also found that confidence-building efforts working with land reform activists on settlement agroforestry projects was a necessary entry-point.

Continuing pressures on forest fragments exist, and efforts to build awareness of the irreplaceable importance of these fragments, also increases pressures. Environmental awareness also highlights the fact that without progress on rural poverty, forest fragments are still a potential “weapon of the weak” (Scott 1985). Though the dwindling, isolated forest fragments in the Atlantic Forest constitute one of the world’s greatest and most immediate risks of biodiversity loss, fragments continue to be a livelihoods buffer for people without economic alternatives during cyclical and sectoral economic adjustment, and can be held hostage by social movements to put political pressure on government to offer better economic alternatives. Despite these structural forces, a surprising degree of mutual interest was discovered in work around protected areas in these three Atlantic Forest regions. As the land reform movement employed technicians and understood the ecological consequences of forest degradation, increasing political efforts and risks were taken to avoid zero-sum confrontations. Environmental

NGOs also learned that their technical capacity to influence public policy in favour of better lands for small-scale agriculture did not contradict their aims of conserving habitat remnants, and could potentially contribute to the reconstruction of habitat connectivity between core refuges for metapopulation management of large and threatened carnivores such as the jaguar in the Atlantic Forest. Therefore, the rest of this thesis considers how jaguars can help as landscape detectives that seek to reduce fragmentation in this critical habitat.

CHAPTER 4

VERIFYING CAMERA TRAPPING DENSITY ESTIMATES OF JAGUAR WITH RADIO TELEMETRY

4.1 Introduction

Radiotelemetry has been extensively used to derive estimates of jaguar density in Latin America, by providing data on home range size and social organization (Sunquist 1981, Smith et al. 1987, Quigley 1993, Crawshaw 2004, Soisalo and Cavalcanti 2006). However, capture-recapture methodology has recently become an important monitoring tool for estimating carnivore density when individually animals can be identified in camera traps (Karanth and Nichols 1998, Carbone et al. 2001, Karanth 2002, Trolle and Kery 2003, Soisalo and Cavalcanti 2006). Jaguars have individually identifiable pelage patterns and are therefore an appropriate species for using camera trap capture-recapture methodology for estimating their population density. The use of camera trapping to estimate jaguar population density has only recently begun in Latin America (Maffei et al. 2004, Wallace et al. 2003, Silver et al. 2004, Soisalo and Cavalcanti 2006).

This study estimated jaguar densities in the same location using both camera traps to estimate capture-recapture rates and radiotelemetry. This represents a rare opportunity to test the reliability of the two methods on a free ranging large carnivore population. Accurate estimates of jaguar abundance in the study areas can also be an indicator of habitat quality, and attention needs to be directed toward the development of suitable techniques for surveying this species. Within the landscape detective approach, initial jaguar abundance in each habitat patch is a determinant variable to evaluate the spatial structure of the jaguar metapopulation. Linked with population viability analysis (PVA) the landscape detective approach uses stage matrix models (Leslie 1940, Akçakaya et al. 2007) to make projections of population’s size and needs density information to specify the initial number of individuals in each age class.

In this study I estimated jaguar density for the Morro do Diabo State Park, Brazil, using both camera trapping and radio tracking methodologies. This is one of the first population estimates of a large carnivore where both methods were implemented simultaneously. The aims of this study were: 1) to estimate jaguar density in the study site using capture-recapture data from camera traps; 2) to estimate jaguar density in the study site using VHF and GPS telemetry data; 3) to compare both estimates; 4) provide accurate density information for the landscape detective modelling approach and, 5) to assess the implications for future jaguar population estimates and for conservation planning.

4.2 Methods

This study was carried out in the Morro do Diabo State Park where detailed information about this specific study site is provided in Chapter 2.

4.2.1 Camera Trapping

The sampling design and statistical methods used in this study were based on tiger studies conducted in India (Karanth 1995, Karanth and Nichols 1998) and on other jaguar studies recently conducted in Latin America (Wallace et al. 2004, Maffei et al. 2004, Silver et al. 2004, and Soisalo and Cavalcanti 2006). Camera trapping was conducted between May and December of 2003. I used 12 CamTrackker units, which combine a 35 mm camera with a passive infrared motion detector that senses heat-in-motion. Cameras functioned with rolls of 36 prints, 400 ASA.

Cameras with the passive infrared motion detector system are easy to set up, but in tropical areas like the Morro do Diabo, the traps may be triggered by shades moving in front of the sensor, such as a tree moving in the wind in front of the sun. In addition, it is difficult for the infrared sensor to sense warm-blooded animals when the temperature is high (Trolle and Kery 2003). To resolve this problem the cameras were programmed to work only during the evening, nights, and early mornings, which in any case suits for crepuscular and nocturnal carnivores like jaguars.

One of the most important aspects for estimating densities with camera trapping is to capture as many different individuals as possible and to obtain as many photo recaptures of each animal as possible (Karanth and Nichols 2002). To obtain adequate numbers of jaguar pictures, camera traps were placed on roads and trails, since jaguars regularly travel along forest roads and previously open trails. The Morro do Diabo has a good road system that allowed a systematic placement of cameras. Park rangers also helped in defining areas that were frequented by jaguars. Traps were attached to trees and placed on both sides of the road to photograph both flanks of each individual to assured individual identification simultaneously.

The number of cameras available is usually the limiting factor for most camera trap studies. However, the sample design dictates that the whole study area is evenly covered with traps and that all individuals within the study area have some chance of being photographed (Karanth and Nichols 2002). A pilot radio tracking study of jaguars at Morro do Diabo showed that the home range of females ranged from 50 km^2 to approximately 100 km^2. Therefore, at least two to three traps were placed in an area of 50 km^2. This design resulted in a distance of about five to 5-7 km between traps. At least 30 traps would be required to cover the entire area of Morro do Diabo simultaneously. Because only 12 cameras were available, the study area was subdivided into smaller sub-sections and each sub-section was sampled independently (Karanth and Nichols 2002, Henschel and Ray 2003). This increased the length of the time required to complete the survey. Therefore, tree similarly-sized contiguous blocks (mean=100 km^2) were sampled sequentially using the 12 traps.

The low capture rate of jaguars was compensated for by boosting the capture effort. This was accomplished by increasing the number of time units in each block and by grouping two consecutive days in each block as a single sampling occasion (Table 1). Traps were set in Block 1 and left for 20 days. Traps were then moved to Block 2 and left for the same number of days as in Block 1. This procedure was repeated for Block 3 and then each block was sampled a second time. The number of captures for occasion 1 was obtained as the total number of captures occurring on the first and second day of trapping in each block. The number of captures/recaptures for occasion 2 was obtained as the sum of capture/recaptures for the third and fourth day of trapping in each block, and so on. This approach yielded 10 sampling occasions for each session. Capture data were analyzed using the program CAPTURE (Otis et al. 1978, White et al 1982, Rexstand and Burnham 1991).

Capture-recapture models have been developed for closed populations and the program CAPTURE gives an estimate of population size (N) and variance for animals within the effective sample area A (W). Animal density is then estimated using D= N/A, where N is population size and A the area sampled. The area used for this calculation is not simply the sampled area (A) encompassing the polygon of the traps, but it is the effective sample area that includes an additional buffer strip around the trap polygon (Karanth and Nichols 1998, Karanth 2002). The buffer strip width was calculated as half of the “mean maximum distance moved” (MMDM) by jaguars photographed on more than one occasion. Areas outside the buffer zone of Morro do Diabo, such as villages, settlements, cattle pastures, agricultural fields, and water courses of the Paranapanema River, were not considered jaguar habitat and were excluded from the effective sample area. (Figure 4.1). The decision to exclude these areas from the MMMD buffer was reinforced by the habitat used by radio collared jaguars. Areas that were never used by the collared animals were not considered potential habitat.

Table 4.1. Sampling effort (number of trap-nights) of the different sampling occasions for estimating jaguar density using camera-traps.

Occasion	**Period in days (DD/MM/2003)**	**Effort (trap-nights)**
1	16/05, 06/06, 27/06, 29/07, 17/10, 20/11 17/05, 07/06, 28/06, 30/07, 18/10, 21/11	144
2	18/05, 08/06, 29/06, 31/07, 19/10, 22/11 19/05, 09/06, 30/06, 01/08, 20/10, 23/11	144
3	20/05, 10/06, 01/07, 02/08, 21/10, 24/11 21/05, 11/06, 02/07, 03/08, 22/10, 25/11	144
4	22/05, 12/06, 03/07, 04/08, 23/10, 26/11 23/05, 13/06, 04/07, 05/08, 24/10, 27/11	144

5	24/05, 14/06, 05/07, 06/08, 25/10, 28/11 25/05, 15/06, 06/07, 07/08, 26/10, 29/11	144
6	26/05, 16/06, 07/07, 08/08, 27/10, 30/11 27/05, 17/06, 08/07, 09/08, 28/10, 01/12	144
7	28/05, 18/06, 09/07, 10/08, 29/10, 02/12 29/05, 19/06, 10/07, 11/08, 30/10, 03/12	144
8	30/05, 20/06, 11/07, 12/08, 31/10, 04/12 31/05, 21/06, 12/07, 13/08, 01/11, 05/12	144
9	01/06, 22/06, 13/07, 14/08, 02/11, 06/12 02/06, 23/06, 14/07, 15/08, 03/11, 07/12	144
10	03/06, 24/06, 15/07, 16/08, 04/11, 08/12 04/06, 25/06, 16/07, 17/08, 05/11, 09/12	144
Total		1440

4.2.2 Radio Telemetry

The camera trapping study was carried out simultaneously with the radio telemetry study in order to compare the same jaguar population in space and time. Seven jaguars were captured using custom-made iron box traps baited with live bait or treed by trained dogs and chemically restrained with Zoletil (tiletamina-zolazepan). The first two jaguars captured were fitted with conventional VHF radio collars made by (Telonics ®). The remaining five jaguars were fitted with Global Positioning Systems GPS Televilt satellite collars to increase the number of locations for each jaguar home range and to reduce project costs by reducing the number of telemetry flights. VHF radio collared jaguars were located approximately once a week resulting in 40-45 locations per year.

Triangulation analysis with the program (TRACKER) was used to compute fixes obtained from all VHF locations. GPS collars were programmed for three locations/day. However, due to the dense vegetation that covers most of Morro do Diabo, these collars were recording approximately four locations/week (200 locations/year). Based on analysis of consecutive locations, these locations were not biased towards particular habitat types. Most locations were independent points, since they were usually separated by 2-3 day intervals. GPS locations from GPS collared animals were downloaded from aircraft at approximately 70-day intervals. All jaguar locations were plotted on a Landsat Satellite Image and home ranges were estimated using the Animal Movement Analysis extension for ArcView GIS 3.3 (Hooge and Eichenlaub 2000). The minimum convex polygon plotting 95% of location data for each individual was used to estimate home ranges and the harmonic mean method was used to remove outliers (Dixon and Chapman 1980).

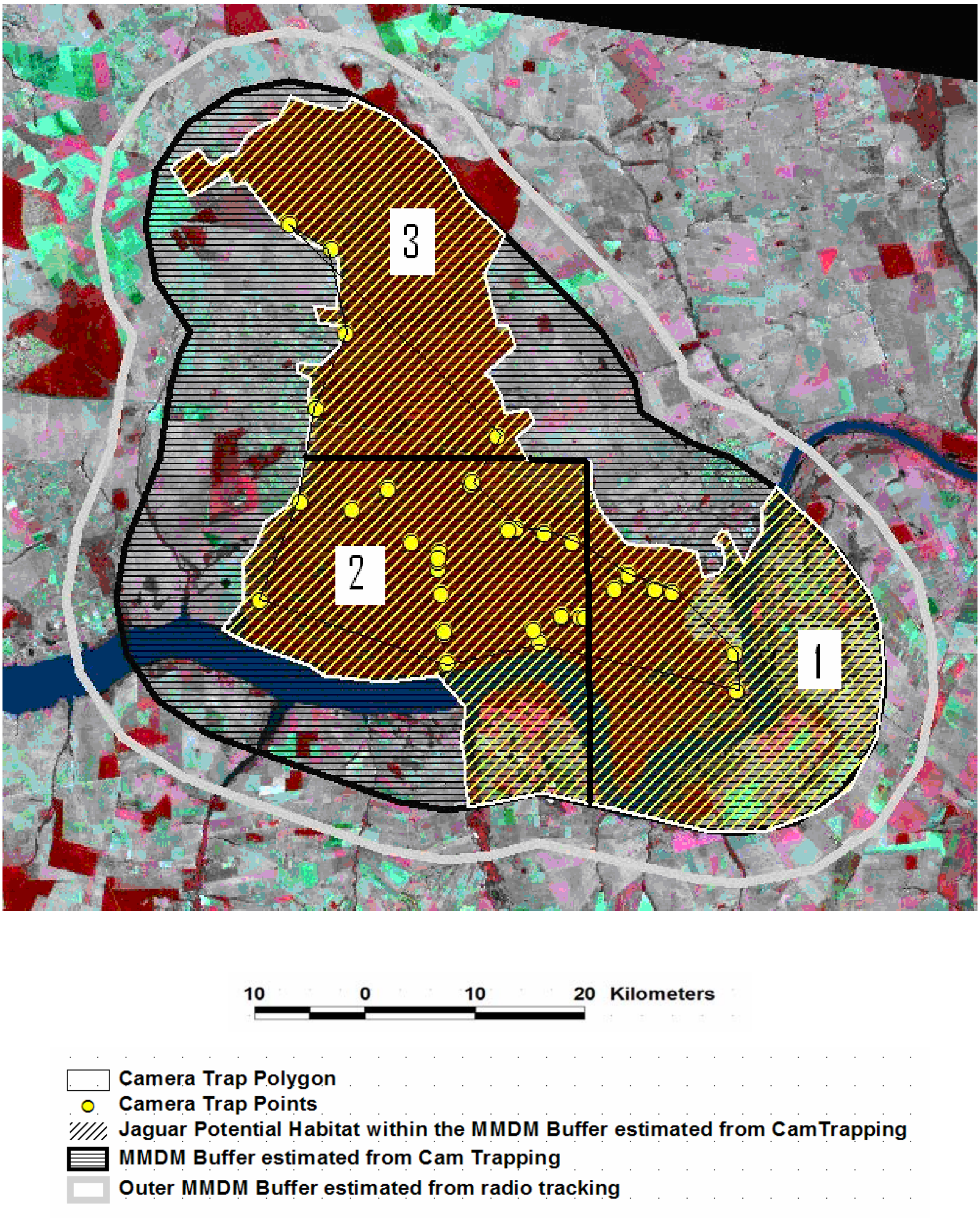


Figure 4.1. A satellite image of Morro do Diabo State Park, illustrating the layout of camera traps, the potential jaguar habitat and the effective sample area from different MMDM buffers. Numbers 1, 2 and 3 are the three different blocks sampled by the camera traps.

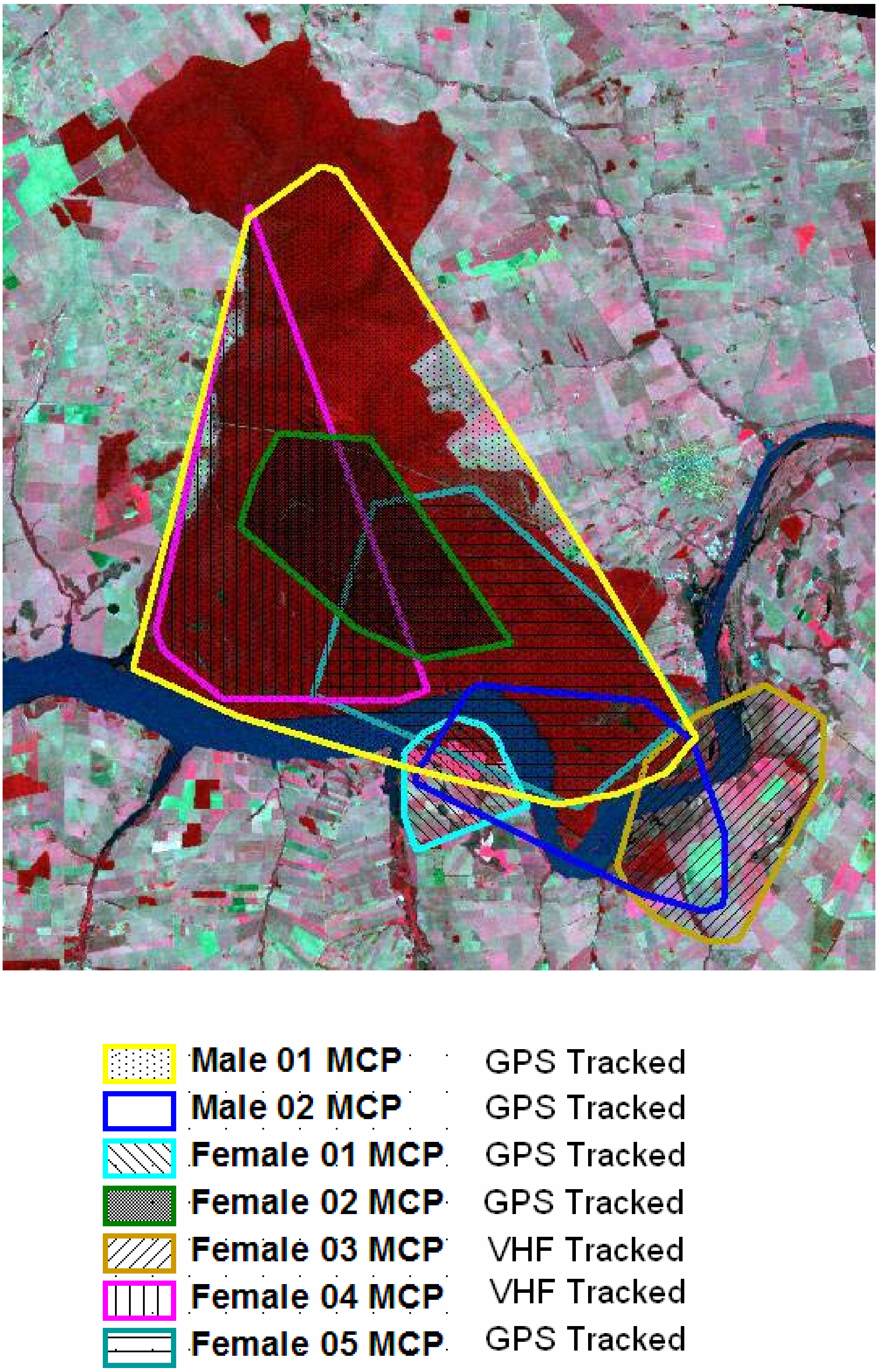


Figure 4.2. Map of jaguar home ranges based on location data and using the 95% minimum convex polygons to delineate each jaguar home range. The area used by the jaguar population determined the perimeter used for density calculations for males and females.

Density estimates of jaguar populations from the radio telemetry study were calculated as the sum of radio collared individuals divided by the area used by these individuals. The area used by the jaguar population was estimated as the total area making up the jaguar home ranges (Figure 4.2). This method of estimating density from radio collared animals takes into consideration the area of overlap between individuals (Crawshaw 1995, Burch 2001). Density of male and female jaguars were estimated separately and then summed, since males tended to have larger home ranges than females and a combined analysis would underestimate jaguar density in the study area.

4.3 Results

4.3.1 Camera Trapping

A total of 10 individual jaguars were positively identified from their distinct pelage using 78 photographs captured during the sampling effort of 1.440 trap-nights, spread over 10 months and 10 sampling occasions (Table 1). The capture sequence of the 10 individually identified jaguars photographed within the study area revealed that 70% were recaptured (Table 2). From these photo, three jaguars were identified as males, six as females and one as undetermined sex with a sex ratio of 1:3. No cubs were photographed. Two (20%) of the jaguars had a melanistic coat coloration, and .it was also possible to confirm the left and the right profiles of some jaguars by the presence of radio collared animals.

CAPTURE generates abundance estimates based on a variety of data models that assume different sources of variability in capture probabilities. The population size estimated from the M_h model (which assumes differing probability of capture between individuals) was 13 jaguars (SE ±2.46) with a 95% confidence interval ranging between 11-22. The estimated probability of capturing an unmarked animal on any trapping occasion (average p-hat) was 0.26. The estimated probability of capturing a jaguar at least once during the entire study period was calculated as $1-(1-0.2615)^{10} = 0.96$. The closure test was consistent with the assumption that this jaguar population was closed for the duration of the study (test in CAPTURE: $z = -0.250$, $p = 0.40$). The discriminant function selection procedure confirmed that the M_o (which assumes no variation in capture probability amongst individuals, or over the course of the study) and M_h models were the most appropriate for this data set. The population estimate derived from the M_h model was selected, because variable probability of capture makes the most inherent biological sense. In addition, the robustness of the Jacknife M_h estimator to deviations from model assumptions was taken into consideration when choosing this model (Otis et al. 1978).

The mean maximum distance moved by all jaguars that were captured in the photographs and in different trap locations was used to calculate the buffer width. The MMDM was 23.18 km for males and 6.67 km for females. The MMDM of all individuals combined was 13.74 km. When halved (6.87 km) and added to the sampled area delineated by the camera trap polygon (Figure 4.1), it produced an effective sample area of 526.17 km^2 of potential jaguar habitat. With an estimated population size of 13 jaguars, this resulted in a density estimate of 2.47 jaguars/100 km^2 (SE ±0.46) (Table 4.3).

Table 4.2. Capture histories of individually identified jaguars in Morro do Diabo Park.

Animal		Capture history [a]
1	adult male, radiocollared	0 0 0 1 0 1 0 1 0 1
2	adult male, radiocollared	0 0 0 0 0 0 1 0 0 0
3	adult female	1 1 1 0 1 0 1 0 1 1
4	adult female, radiocollared	0 0 0 0 1 0 1 0 0 1
5	sub adult male	0 0 0 1 1 1 1 0 0 1
6	sub adult male	0 0 1 1 1 1 0 1 1 1
7	adult female, radiocollared	1 0 0 0 0 0 0 0 0 0
8	sub adult female	0 0 0 0 0 0 1 1 1 0
9	sub adult male	1 0 0 0 0 0 0 1 0 0
10	sub adult undetermined sex	0 0 0 0 0 0 1 0 0 0

[a] 1, capture; 0, no capture. The ten sequential positions represent the successive sampling occasions demonstrated in table 1.

Table 4.3 Density and MMDM estimates of jaguars in the Morro do Diabo State Park using two different methods.

Method	MMDM (km)		Density
	Males	Females	(jaguars/100 km^2) (CI)
Camera Trapping	23.18	6.67	2.47 ± 0.33
Radio Tracking	25.56	15.65	2.20 (N/A)

4.3.2 Radio Telemetry

Radio telemetry locations of 2 adult males and 5 adult females were used to calculate the home range of jaguars and estimate their density (Table 4.3). Ground triangulation and telemetry flights for the VHF collars together with downloaded GPS locations produced a total of 717 jaguar locations, comprising 85% GPS locations and 15% VHF locations. The number of locations used to calculate home ranges for the collared jaguars averaged 102 locations/jaguar and varied from 28 to 214 point localities.

Home range estimates (95% MCP) varied considerably between the jaguars, and ranged from 18.95 km^2 for female 01 to 339.24 km^2 for male 01. The mean maximum distance moved (MMDM) was 25.56 km for males and 15.65 km for females. The MMDM of all individuals combined was 18.48 km (Table 4.3). Average home range size was 207.06 km^2 (n=2) for males and 75.20 km^2 for females (n=5) (Table 4.4). Average overlap area was 38.11 km^2 (18%) for males and 20.22 km^2 (26%) for females. The total area used by the male jaguars was 383.03 km^2 resulting in a density of 0.53 males/100 $km^{2.}$ The total area used by the female jaguars was 301.27 km^2 resulting in a density of 1.67 females/100km^2. When combined, the overall density of jaguars in the study area was 2.20 jaguars/100 km^2 (Table 4.3). Based on confidence interval inference there is no statistical difference between density estimates of jaguars using camera trapping (2.47 ind/100km^2) and radio telemetry (2.20 ind/100km^2) (Table 4.3).

Table 4.4. Home range sizes, weight and number of locations for radio-collared jaguars in the Morro do Diabo State Park.

Jaguars	Weight (kg)	N. of locs	Home range sizes (km^2) (95% MCP)
Female 01	68	92	18.95
Female 02	59	28	57.06
Female 03	56	214	60.07
Female 04	86	36	119.13
Female 05	55	29	120.82
Male 01	90	156	339.24
Male 02	98	162	74.89

4.4 Discussion

To my knowledge this is one of the very few jaguar field studies in the Neotropics where camera trapping and radio tracking methodologies have been used simultaneously to estimate population density in the same study area. Jaguar densities have traditionally been difficult to study because of the cryptic nature of the species and their low population densities. The comparison of camera trapping and radio telemetry techniques used in this study have produced comparable estimates of jaguar densities (Table 4.3).

The long time period necessary to achieve sufficient camera trapping sampling occasions from May to December, might have violated the assumption of a closed population. However, the closure test showed no evidence that this jaguar population was in violation of this assumption. This could be due to the fragmented nature of the jaguar population in Morro do Diabo. Silver et al. (2004) used an index of jaguar abundance based on trapping rates and calculated the mean number of jaguar pictures per 100 trap nights. Their highest reported abundance was 3.49 jaguar/100 trap nights and the average of five sites in Bolivia and Belize was 2.06 jaguar/100 trap nights. Results from Morro do Diabo showed more frequent capture of jaguar with of 5.41 jaguar pictures/100 trap nights, which suggests that a high proportion of the population was recorded. Jaguar cubs were not captured by the cameras, but direct and indirect observations confirm that they exist in Morro do Diabo. Deliberate avoidance of traps by cubs or by their mothers and other behavioural differences between young and adult individuals usually result in cubs having extremely low capture probabilities with camera traps (Karanth 2002).

The population estimates of adults and sub adults jaguars from Morro do Diabo were 2.20 individuals/100 km^2 based on radio tracking and 2.47 individuals/100 km^2 based on camera trapping. These densities are at the low end of estimates from other jaguar populations in South and Central America. For example, in Iguaçu National Park in Paraná State, Brazil, jaguar density was estimated at 3.70 individuals/100 km^2 (Crawshaw 1995). In the Brazilian Pantanal, the jaguar density was estimated at 2.90 individuals/100 km^2 (Schaller 1983, and Schaller and Crawshaw 1980) and 6.50 individuals/100 km^2 (Soisalo and Cavalcanti 2006). In Belize, jaguars 20-30 jaguars were present in a 250 km^2 area, resulting in a density of 8 individuals /100 km^2 (Rabinowitz and Nottingghan 1986). Silver et al. (2004) used camera trapping to census jaguars in the rainforests of Belize, dry forests of the Chaco, and Amazonian rainforests of Bolivia and found densities ranging between 2.84 to 8.80 adult individuals per 100 km^2. The lower jaguar densities in Morro do Diabo Park compared to other sites in South and Central America is likely due to the semideciduous habitats. In these habitats, primary production is lower and more erratic than in the moister forests, and availability of water is lower, thus affecting the distribution and density of prey species (Cullen et al. 2001). The moist tropical forests and alluvial marshlands of tropical South America probably correspond to the Upper limit of jaguar densities, whereas the semideciduous habitats and *Cerrado* vegetation may correspond to the lower limits.

Estimates of MMDM (mean maximum distance moved) are calculated from photo captures when information on MMDM is not available from radio tracking studies (Karanth 1995, Karanth and Nichols 2002, Silver et al. 2004, Soisalo and Cavalcanti 2006). Thus, half of the average maximum linear distance of jaguar movement from one trap to another is calculated and used to determine the buffer width and sampling area. Soisalo and Cavalcanti (2006) have shown that camera trapping renders a biased representation of jaguar movement, whilst information from radiotelemetry more accurately represents animal movements (Table 4.5). Their results showed that jaguars had moved linear distances which were twice as as the distances estimated by the MMDM of photo captures. Therefore, Soisalo and Cavalcanti (2006) suggest that the MMDM estimated from the camera traps can under-estimate maximum distance moved by jaguars and consequently inflating jaguar density estimates. For example, results of their study in Pantanal showed that the MMDM buffer obtained from camera traps was 3.0 km and the MMDM obtained from GPS radiotelemetry was 5.2 km, or 73% greater (see different MMDM buffers in Table 4.5).

Results of my study in Morro do Diabo show similar trends. The MMDM obtained from camera traps was 13.74 km and the MMDM from VHF/GPS radiotelemetry was 18.48 km, or some 34% larger (Table 4.3). The MMDM of female jaguars showed the largest differences with 3.33 km from camera trapping and 7.82 km from radiotelemetry. If the MMDM buffers of appropriate jaguar habitat were used from photo capture the density from the camera trapping would be overestimated. The estimated area used by jaguars calculated only from camera traps (845.07 km^2) would represent only 74% of the true jaguar ranges calculated by the VHF/GPS telemetry (1137.17 km^2). It is recommended that camera trapping methodology should be used in conjunction with other monitoring techniques that better reflect the true ranges of animals to estimate the effective sample area so that density estimates can be adjusted accordingly.

Table 4.5. Effectively sampled areas calculated from camera trap and GPS/VHF-telemetry, and the resulting jaguar density estimates (Soisalo and Cavalcanti 2006, and this study)

Survey Year	Sample area size (km^2) outer trap polygon	Method used for buffer width calculation	Buffer width (km)	Effective sampled area (km^2)	Resulting density estimate (jaguars / 100 km^2
2003	165	*Camera traps*			
		MMDM	3.0	360	10.3 ± 1.53
		Full MMDM	6.0	653	5.7 ± 0.84
		GPS telemetry			
		Actual MMDM	5.2	568	6.5 ± 0.97
		Home Range	5.1	557	6.6 ± 0.99
2004	110	*Camera traps*			
		MMDM	2.9	274	11.7 ± 1.94
		Full MMDM	5.8	554	5.8 ± 0.97
		GPS telemetry			
		Home range	5.1	476	6.6 ± 1.13
This Study	225	*Camera Traps*			
		MMDM	6.9	526	2.47 ± 0.46
2003		*GPS telemetry*			
		Actual MMDM	9.2	1137	2.20

Based on my estimates, the 370 km^2 of potential habitat in and around Morro do Diabo State Park should support a jaguar population of not more than 15 adult individuals. This very small population of jaguars, even in quality habitat, coupled with their low reproductive potential, demonstrates the problem of conserving this particular population. Some eminent major threats faced by this population include habitat isolation, poaching, limited dispersal, road mortality and genetic isolation. Very large tracts of land in an interconnected land mosaic must be preserved to ensure survival of a viable population. Therefore, the habitat-based population viability analysis within the landscape detective approach is an important tool to rescue the Morro do Diabo population from extinction, by incorporating other identified suitable patches and jaguar populations into the analysis. This should include spatial variation and interaction among all identified populations, geographic configuration of suitable patches, dispersal and spatial correlation that could point to recovery strategies for the whole metapopulation.

The two areas identified as important Jaguar Conservation Units in the vicinity of the borders of Argentina, Brazil and Paraguay (Figure 2.2) comprise an area of approximately 25.000 km^2 of protected and semi-protected habitats (Di Bitetti et al. 2003). Using the jaguar density estimates of this study, we could estimate a potential jaguar metapopulation of at least 500 individuals, excluding cubs. Conservation biologists who manage small and isolated forest fragments must deal with the dynamics of small populations and have an idea of the number of individuals needed within a particular area to ensure that the population will still be thriving in 100 years or more. Although there has been much discussion over the optimum numbers of individuals needed to maintain a population over a hundred year period (Lande 1995, Lynch and Lande 1998), the 50-500 rule is still the most commonly accepted (Hunter 1996). This rule states that a local population of 50 effective individuals (i.e. about 500 actual individuals) is a reasonable minimum viable population size (MVP). Thus, the Upper Paraná Atlantic Forest Ecoregion, along the border of Argentina, Brazil and Paraguay could potentially harbour a viable metapopulation of jaguars. This contradicts the pessimistic scenario posed by Sanderson et al. (2002), and the results of this study clearly show that conservation efforts in the Atlantic Forests of Brazil should remain a high priority for investments in conservation of jaguar and ecosystem biodiversity.

Camera-trapping in conjunction with other methods will be used to continue long-term jaguar monitoring at Morro do Diabo State Park and other areas along the Upper Paraná JCU. Density estimates from multiple sites, including protected areas along the Upper Paraná JCU (e.g. Ivinhema State Park and Ilha Grande National Park) will provide additional jaguar density estimates for the region. Camera trapping is an excellent long-term monitoring method, since replications after long time intervals (e.g. years) can lead to a robust capture-recapture design. These data can then be used to estimate survival and dispersal rates, which can be incorporated into the landscape detective approach and the metapopulation conservation program for the species, providing support for the setting of new protected areas. Camera trapping is currently the only systematic population survey technique for jaguars, and can potentially be applied to other species with individually recognizable markings. This comparative study revealed good prospects for future calibration of camera trapping, and the continued development of the method that will give field workers a valuable and cost effective tool for studying populations of elusive species such as the jaguar.

CHAPTER 5

HOME RANGE AND MOVEMENTS OF ADULT JAGUARS IN THE UPPER PARANÁ RIVER

5.1 Introduction

The jaguar (*Panthera onca*), the largest cat in the Americas and the only living representative of the genus *Panthera* in the new world, historically ranged from the far south-western United States to southern Argentina (Guggisberg 1975). Like most large carnivore species, jaguars are declining throughout their current range and have been eliminated from parts of their historic range (Nowell and Jackson 1996, Swank and Teer 1989, Sanderson et al. 2002 a). Intense persecution of the jaguar in South America, over exploitation of its prey and habitat loss across most its range, has reduced the species to approximately 7.28 million km^2, or only 38% of their historic range (Marieb 2005). Nevertheless, jaguars still persist in an incredible array of habitat types, from tropical moist forests, to xeric shrub lands, to tropical dry forests, to grasslands and savannas (Sanderson et al. 2002 b). The once extensive jaguar habitat of the semideciduous Atlantic Forest in Brazil has been increasingly fragmented and degraded and today only about 8% of the natural habitat remains.

Wide-ranging carnivores with large home ranges, such as the jaguar, are difficult to conserve (Woodroffe and Ginsberg 1999). When faced with human impacts, top carnivores are generally the first ones to go locally extinct. Another implication of large home range size is that many suitable habitat patches, whether jurisdictional or management unit, may not be large enough to support viable or ecologically functional populations of wide-ranging species (Ortega-Huerta and Medley 1999). Therefore, landscape connectivity is viewed as a top priority for large carnivore management, not just for population persistence (Briggs 2001). Another important variable related to home range area is dispersal distance (Delibes et al. 2001, Fahrig 2001; Singer et al. 2001). Just as individual movements within their home ranges can functionally link landscape elements, so can dispersal (McCullough 1996, Brooker et al. 1999, South 1999; Novaro et al. 2000).

Accurate information on home range and movements is crucial for the concept of focal species (Miller et al. 1999, Sanderson et al. 2002) and, therefore for developing the landscape detective approach. In the landscape detective approach, the link between suitable patch analysis and metapopulation viability analyses is characterized by two parameters: threshold habitat suitability and neighbourhood distance. The threshold habitat suitability is defined as the minimum habitat suitability value below which the habitat is not suitable for reproduction and/or survival of the species. A habitat suitability threshold value is determined from jaguar home range size and location. The neighbourhood distance is used to identify nearby GIS grid cells that belong to the same patch (i.e., subpopulation) and represents the movements and foraging distances of the species. Home range and movements data are incorporated in the landscape detective analysis.

Selected areas of concentrated use by an individual within home ranges are often denoted as core areas (Kaufman 1962) implying that these selected areas are of greater significance to the animal. Jaguar home range sizes vary throughout the species geographic distribution (Crawshaw et al. 2004). Most previous studies have reported that males maintain larger home ranges than females and have observed seasonal variation in home range size (Schaller and Crawshaw 1980, Rabinowitz and Nottingham 1986, Crawshaw and Quigley 1991, Crawshaw 1995, Ceballos et al. 2002, Scognamillo et al. 2002, Crawshaw et al. 2004 and Silveira 2004).

Quantitative information on home range and movements of jaguars living in the semideciduous Atlantic Forest habitats in Brazil has lagged behind studies of jaguars in tropical moist forests. Information on jaguar habitat use, home range and movements is important for managing the impact of hunting and trapping of jaguars, jaguar attacks on cattle stock (Crawshaw 2004), the impacts of habitat fragmentation (Cullen et. al. 2005) and for developing habitat suitability models for large scale conservation (Akçakaya 2004).

For any carnivore, the home range size should be related to distribution and density of prey and the season of the year (Sunquist et al. Sunquist 1999). Therefore, critical questions for jaguar conservation are: (1) does jaguar home range vary seasonally? and (2) how does home range size relate to habitat/prey parameters? Although these questions may appear merely academic, they relate directly to space requirements and therefore to conservation strategies for viable jaguar populations in the Upper Paraná River.

I used data from VHF and GPS radio tagged jaguars to quantify jaguar home range and movements, to develop the landscape detective tool and, to test whether jaguar home ranges vary seasonally and if the home ranges relate to prey abundances and distribution. I also compare jaguar home range in the Upper Paraná River to other existing jaguar studies in the Neotropics.

5.2 Methods

This study was carried out in the Morro do Diabo State Park in the State of São Paulo and in Ivinhema State Park State Park in the State of Mato Grosso do Sul. Detailed information about these two specific study sites is provided in Chapter 2.

5.2.1 Radiotelemetry and Home Range Delineation

Between April 1998 and August 2005, 10 adult jaguars (> 2 years old) were captured, radio-collared, and monitored, seven at the Morro do Diabo State Park (MDSP) and three at Ivinhema State Park (ISP). Individuals were captured using custom-made iron box-traps baited with live bait or treed by trained dogs and chemically restrained with Zoletil (tiletamina-zolazepan). The first two jaguars captured at MDSP and the first jaguar captured at ISP were fitted with conventional VHF radio collars made by (Telonics ®). The remaining jaguars were fitted with Global Positioning Systems GPS Televilt satellite collars to increase the number of locations for each jaguar home range and to reduce costs of aerial monitoring. VHF radio-collared jaguars were located approximately once a week resulting in 40-45 locations per year. Triangulation analysis with the program

TRACKER was used to compute fixes obtained from all VHF locations. GPS collars were programmed for three locations/day. However, due to the dense vegetation that covers most of Morro do Diabo, these collars were recording approximately four locations/week (200 locations/year). At ISP, where vegetation is less dense, the GPS collars were performing better and recoding 14 locations/week (700 locations/year). Based on analysis of consecutive daily locations, these locations were not biased towards particular habitat types. Most locations were independent points, since they were usually separated by 2-3 day intervals. GPS locations were downloaded from aircraft at approximately 70-day intervals.

Home range size and movements were analysed separately for the dry season (April-September), the wet season (October-March), and for both seasons combined data were pooled across >1 year of observation. Thus, a dry season home range includes locations for two or more dry seasons for a particular animal. All jaguar locations were plotted on a Landsat Satellite Image and home ranges were estimated using the Animal Movement Analysis extension for ArcView GIS 3.3 (Hooge and Eichenlaub 2000). Annual and seasonal 50%, 85%, and 95% fixed kernel home ranges were calculated for each individual (Worton 1989) with a level of smoothing selected by the least-squares cross-validation (Worton 1987, Seaman and Powell 1996, Seaman et. al. 1999) and a grid cell size of 30 m x 30 m. Kernel estimators are nonparametric, can estimate densities of any shape (Seaman and Powell 1996), and are not influenced by effects of grid size or placement (Silverman 1986). I report the 50% home range as an area of core utilization and the 85% home range as an area of ecological importance for a jaguar. I also report the 95% home range as a commonly referenced contour, but agree with Seaman et al. (1999) that it is of little biological significance and unreliable, regardless of the home range estimator used. Seasonal home ranges were calculated for all individuals, but for statistical comparisons I used only individual adult jaguars, which had ≥ 30 locations in the season. I tested for differences in seasonal 85% home range sizes using a Wilcoxon signed-rank test (T = test statistic). For both sexes, I calculated overlap among annual 85% home ranges.

5.2.2 Radiotelemetry and Movements

For the VHF and GPS-marked animals, linear distances between simultaneous locations were used to calculate the mean and maximum distance moved by the animals. I recognize that some calculations for VHF-marked animals could be underestimated, because data could not be collected on any movements they made out of the study area or telemetry range. Distances were estimated using the Animal Movement Analysis extension for ArcView GIS 3.3 (Hooge and Eichenlaub 2000). I tested for differences in animal movements using Students T-test.

5.3 Results

5.3.1 Home Range Sizes

In Morro do Diabo, the annual 85% home range averaged 162 km^2 (50-275 km^2) for two adult male jaguars and 60 km^2 (SD = 63 km^2) for five adult females (Table 2 Figures 5.2-5.10). For the dry season, males had home ranges 6 times larger than females (158 km^2 x 27 km^2, respectively) (T= 1.12, P = 0.37). For the wet season males had home ranges 2.5 times larger than females (T= 1.16, P = 0.30). However, I caution that the small sample sizes did not allow meaningful statistical comparisons at this level. In Ivinhema Ecological Station, the only male monitored had a yearly 85% home range of 147 km^2, while for the two females yearly home ranges that averaged 130 km^2 (SD = 61). When data from both sexes and study areas are combined in the analysis, dry season 85% home ranges averaged 102 km^2 (SD = 78) and wet season home ranges averaged 85 km^2 (SD = 61), which were not significantly different (T = 14.00, P = 0.31, n = 9 individuals) (Table 4.1, Figures 5.2-5.10).

Table 5.1. Home range areas (km^2) for 3 adult male and 7 adult female jaguars in Morro do Diabo State Park and Ivinhema State Park (1998-2005), using a fixed-kernel estimator.

Animal ID	Years tracked	Annual home range				Dry-season home range				Wet-season home range			
		No. loc.	50%	85%	95%	No. loc.	50%	85%	95%	No. loc.	50%	85%	95%
Morro do Diabo State Park													
M1	1	162	14	50	89	88	6	44	85	74	15	52	86
M2	1	156	55	275	471	138	42	272	478	18	30	127	255
F1	1	92	2	9	18	58	1	5	12	34	7	20	37
F2	2	17	35	98	129	-	-	-	-	17	35	98	129
F3	5	35	47	131	192	24	40	105	143	11	38	203	305
F4	2	214	12	41	65	131	15	49	77	83	5	21	34
F5	1	18	18	80	121	18	18	80	121	-	-	-	-
Male mean		159	34	162	280	113	24	158	281	46	15	52	86
Female mean		75	20	60	92	58	8	27	44	36	6	20	36
Ivinhema State Park													
M3	2	799	20	147	299	399	31	157	295	400	21	139	290
F6	4	326	7	87	135	148	31	89	152	179	6	68	119
F7	1	183	26	173	289	154	24	125	241	30	18	45	63
Male mean		404	20	147	299	299	31	157	295	300	21	139	290
Female mean		254	16	130	212	151	27	107	196	104	12	56	91

* For calculation of averages I included only those jaguars with ≥ 30 locations.

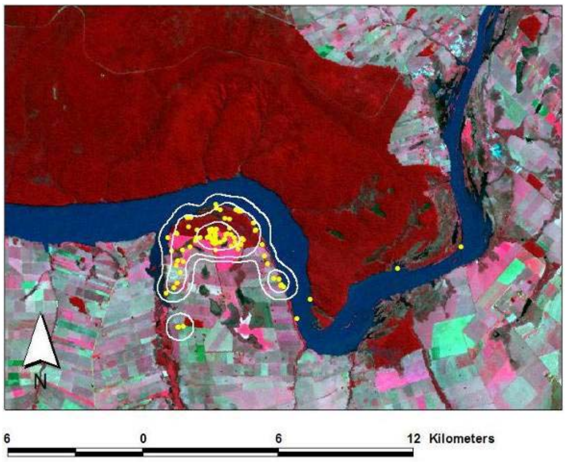
5.3.2 Individual Jaguar Home Ranges and Overlaps

The overlap in annual 85% home ranges with the neighbouring adult females was calculated in the Morro do Diabo State Park for 5 females followed for more than 1 year. For 4 pairs of neighbouring females, mean overlap was 25%. For a single year (2003), overlap in the annual 85% home range of the 2 males averaged 32%. In Ivinhema Ecological Station the overlap in yearly 85% home ranges for the two neighbouring adult females monitored was 15 %.

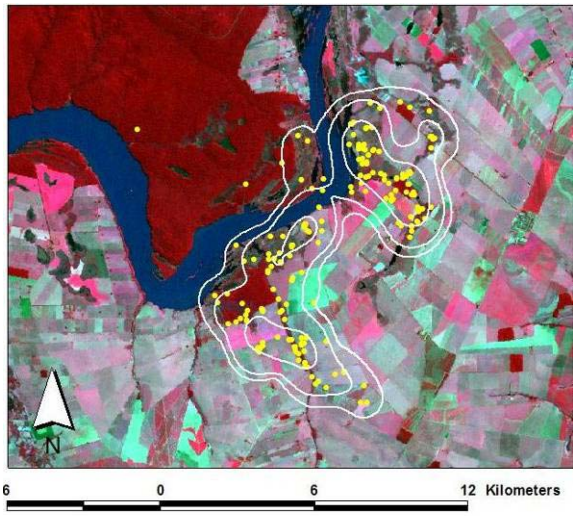
Home range and core area estimates (50%, 85% and 95% fixed-kernel estimator) of individual jaguars and some of their peculiarities deserve further considerations. For example, F1, F4 and M1 tracked in Morro do Diabo State Park had smaller 85% home ranges than the overall average home range for this study area (33 Km^2 versus 110 Km^2). Although this difference could be related to the short monitoring period of F1, their home range and movements seem to be influenced more by human activities (Figures 5.1). For these three individuals, parts of the core 50% area overlapped extensively. These areas of overlap mainly comprised a small 400 ha isolated forest fragment and some remaining gallery forest corridors across the Paranapanema River, outside Morro do Diabo in the southern edge of the Park. These areas are privately owned by the Copacabana Farm and on several occasions the neighbouring rancher complained about jaguars. For example, in 2004, 56 head of cattle were reported killed by jaguars in this area. This individual core areas also seem to be linked to the presence of cattle, which attracted already habituated jaguars to areas of “easy prey”, further explaining their smaller home ranges and smaller distances moved.

All other tracked jaguars in Morro do Diabo established their core areas within the limits of the park, and avoided the periphery. These adult jaguars covered mostly central areas of Morro do Diabo, which is largely undisturbed and still supports a good density of native ungulates (Cullen et al. 2001). Female 2 ranged mostly in the southern areas of Morro do Diabo, and her home range fixes shows that the paved road that crosses the park bisects her 85% fixed Kernel home. In November 2002, female 2 was hit by a car on this road and died, which explains her small sample size. Female 3 established her 85% fixed kernel home range in the western portion of Morro do Diabo, frequently using an internal and unpaved road as a main travel route. This resulted in many camera traps photographs of this individual. Her proximity with a rural settlement on the edge of Morro do Diabo also generated some complaints by the neighboring settlers due to supposed predation on domestic animals.

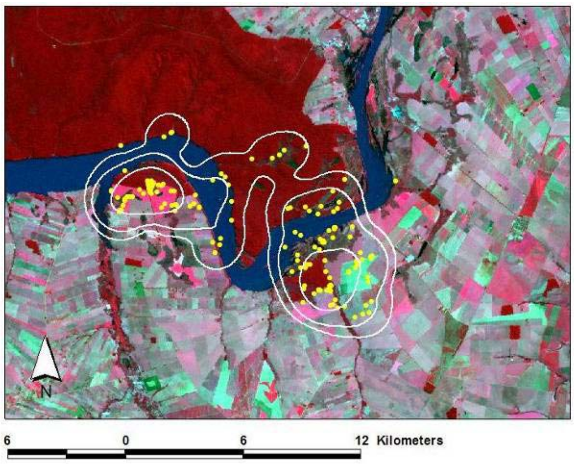
In Ivinhema State Park, the core 50% areas of M3 and F6 overlapped intensively, but were located within the Ivinhema borders. These 50% areas are composed mainly of a mosaic of open marshlands and pastures where cattle are still abundant inside the Park. Both in Morro do Diabo and in Ivinhema, males were found more often at greater distances from the center of their core 50% ranges than females (Figures 5.1-5.10). The distribution of locations in relation to the center core areas shows a tendency of greater use of the periphery of the home ranges for adult males. The adult females, on the other hand, displayed a more regular pattern of use in their areas.



Female 1 (F1)



Female 4 (F4)



Male 1 (M1)

Figure 5.1. Home range and core area overlaps of F1, F4 and M1 in Morro do Diabo State Park.

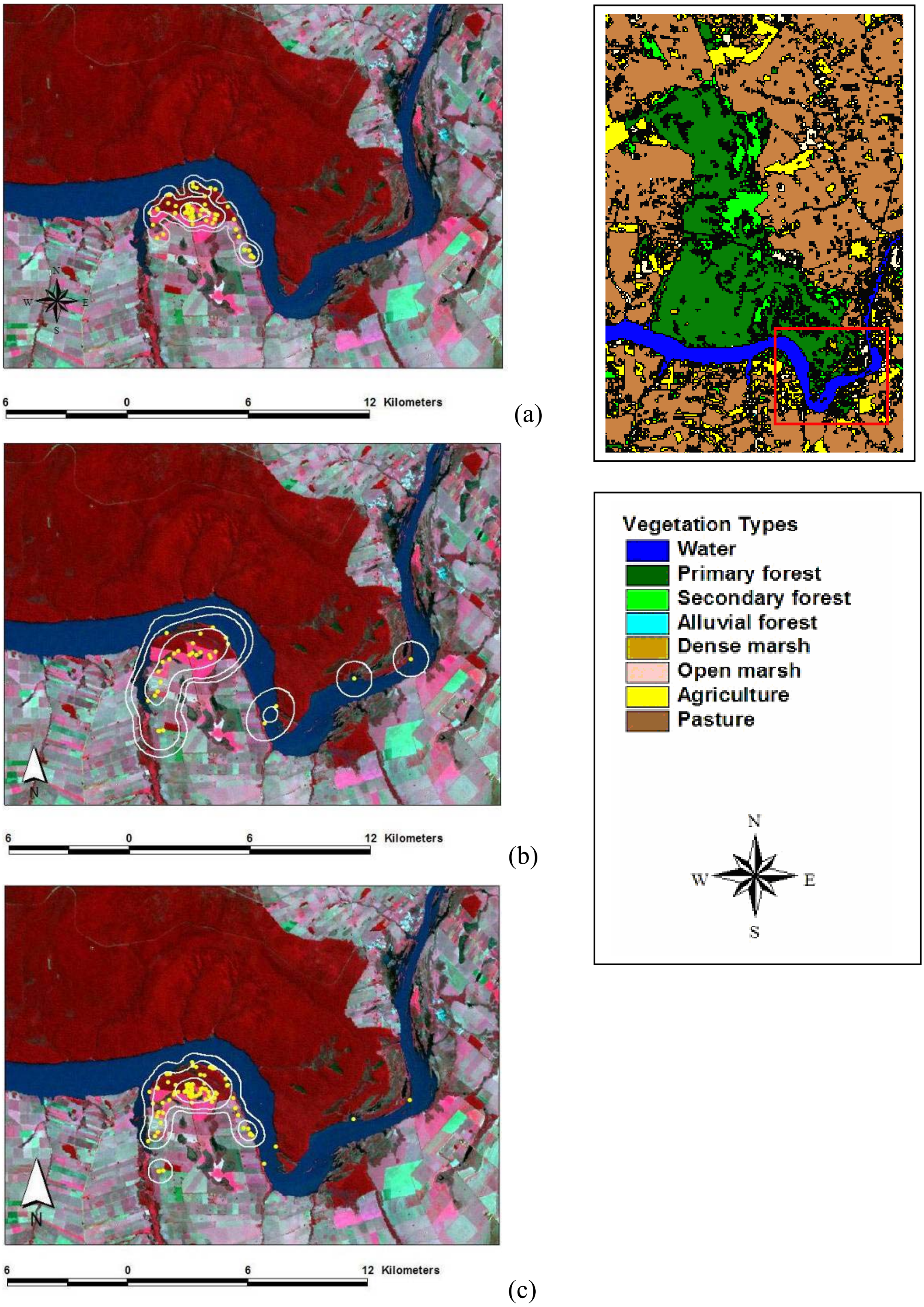


Figure 5.2. a) Dry season, b) wet season and c) annual 50, 85 and 95% fixed kernel home ranges and locations of adult F1 in the Morro do Diabo State Park.

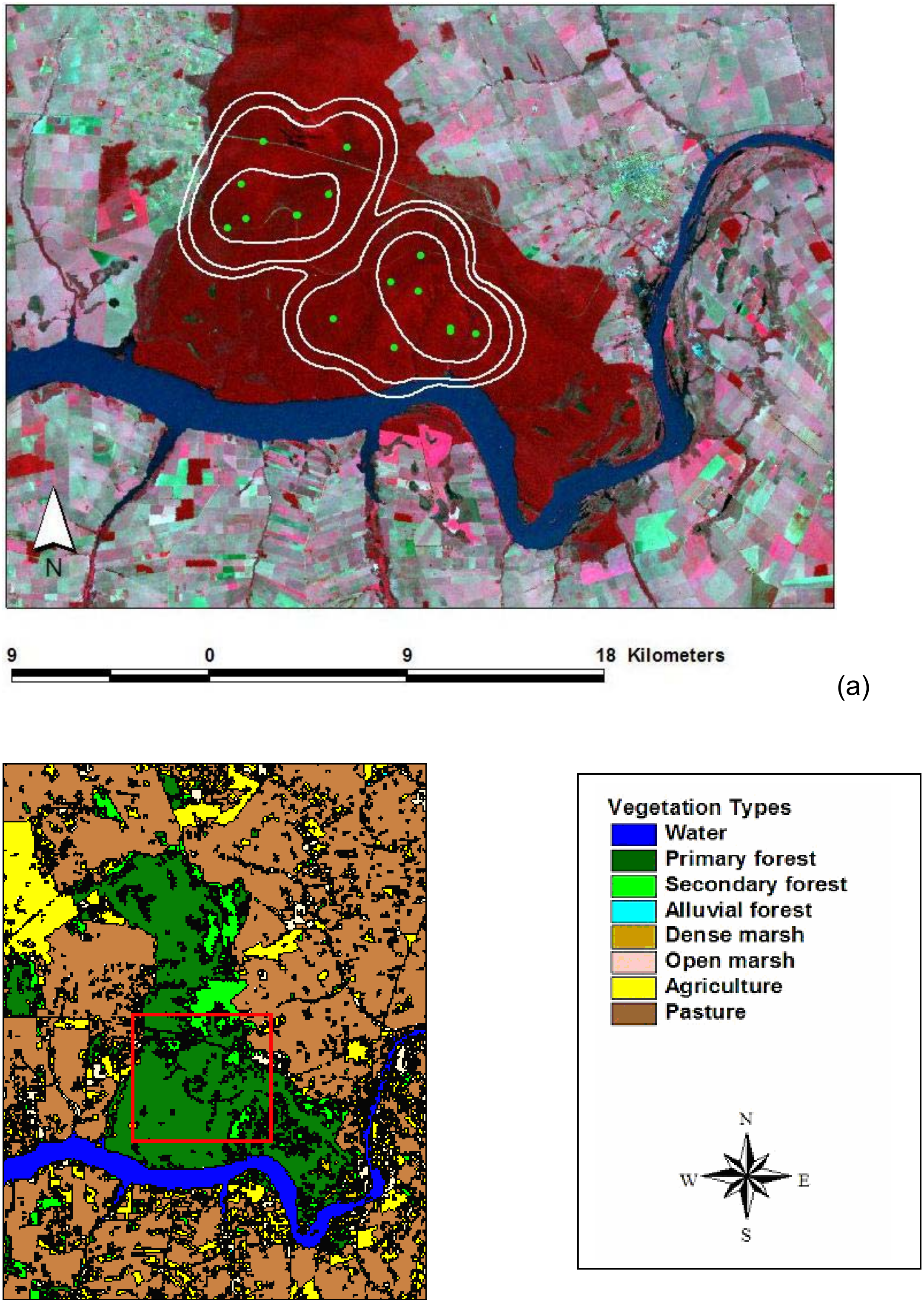


Figure 5.3. a) Wet 50, 85 and 95% fixed kernel home ranges and locations of adult F2 in the Morro do Diabo State Park. Home ranges were estimated using only 17 locations from the dry season.

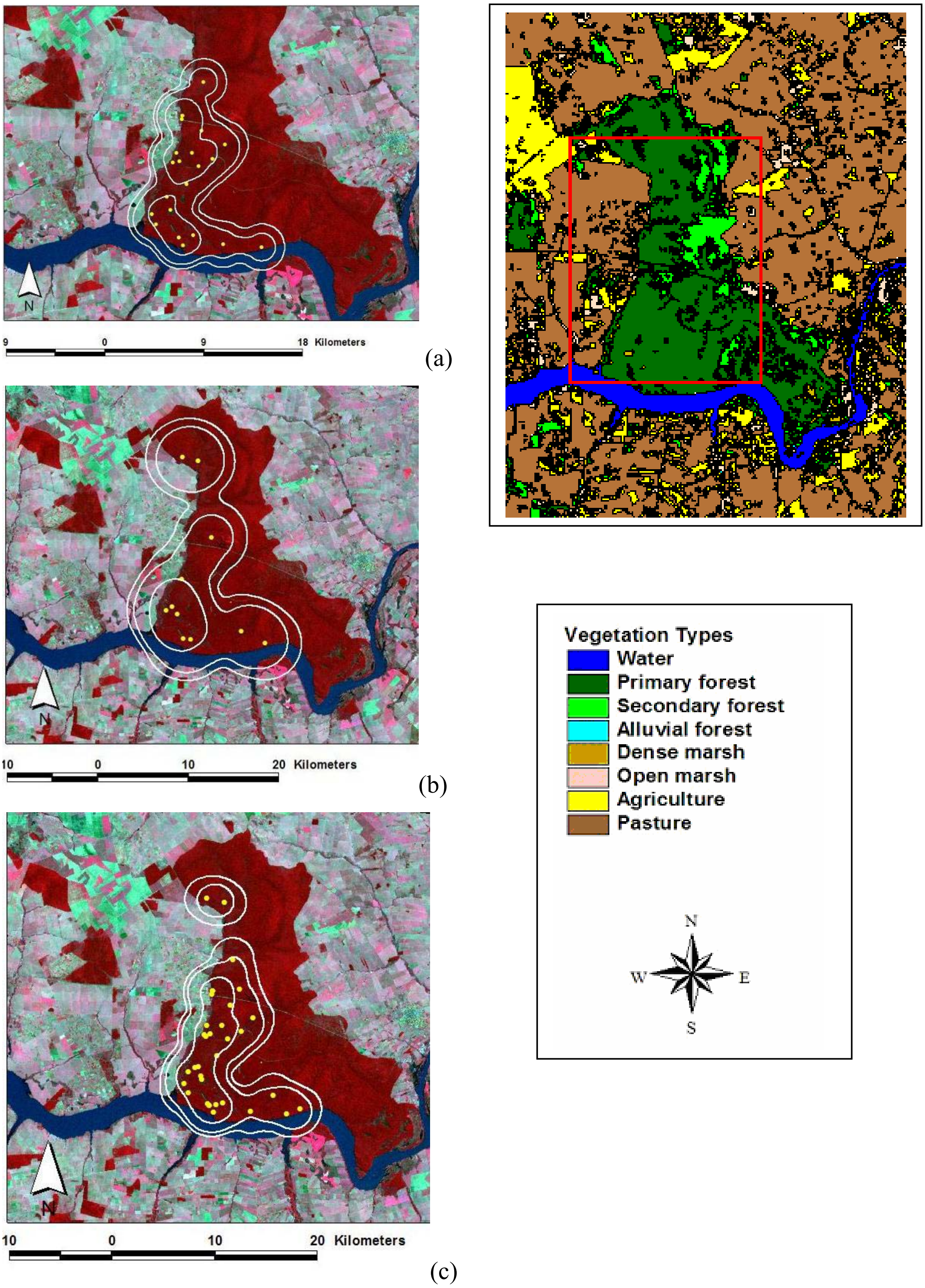


Figure 5.4. a) Dry season, b) wet season and c) annual 50, 85 and 95% fixed kernel home ranges and locations of adult F3 in the Morro do Diabo State Park.

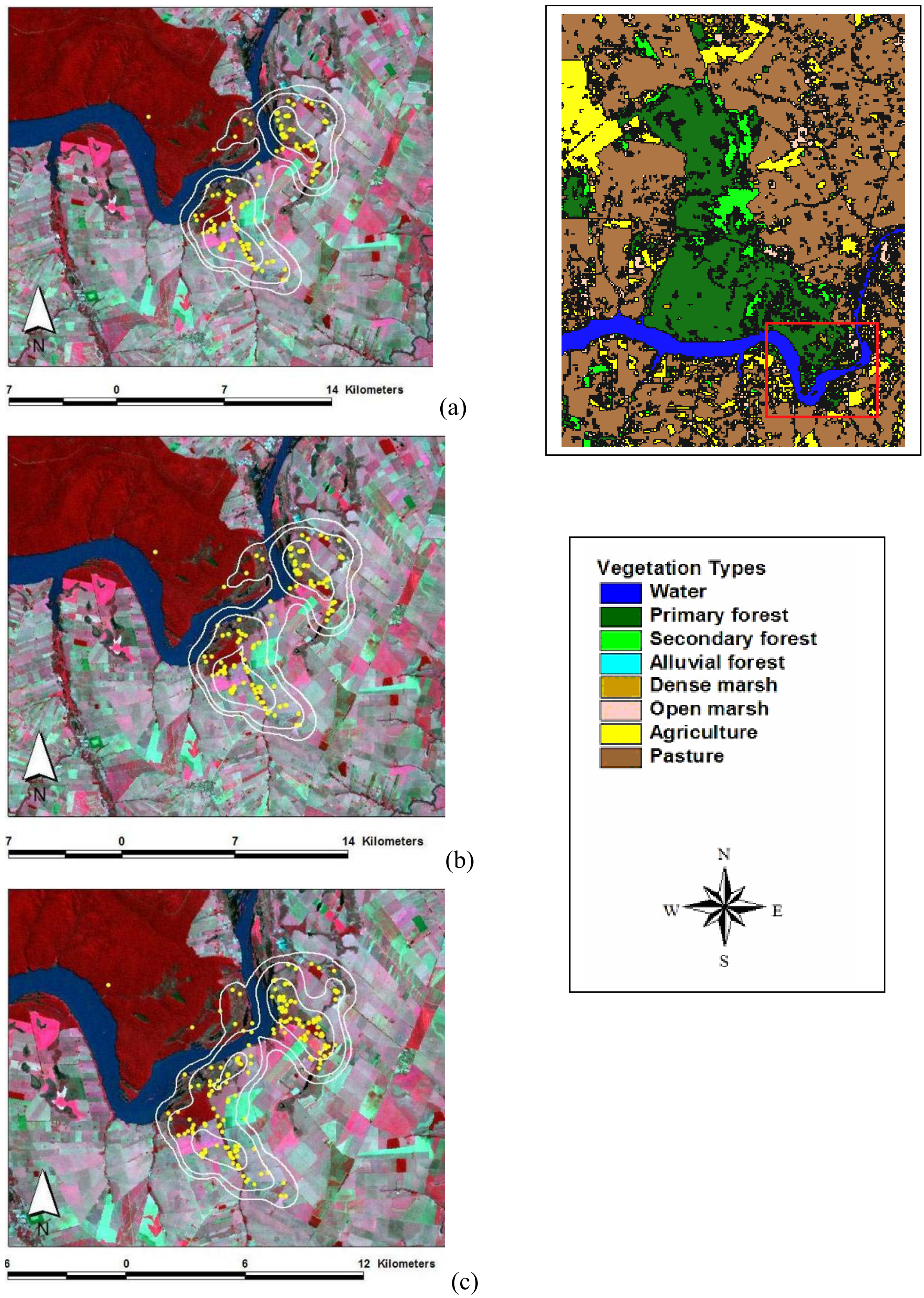


Figure 5.5. a) Dry season, b) wet season and c) annual 50, 85 and 95% fixed kernel home ranges and locations of adult F4 in the Morro do Diabo State Park.

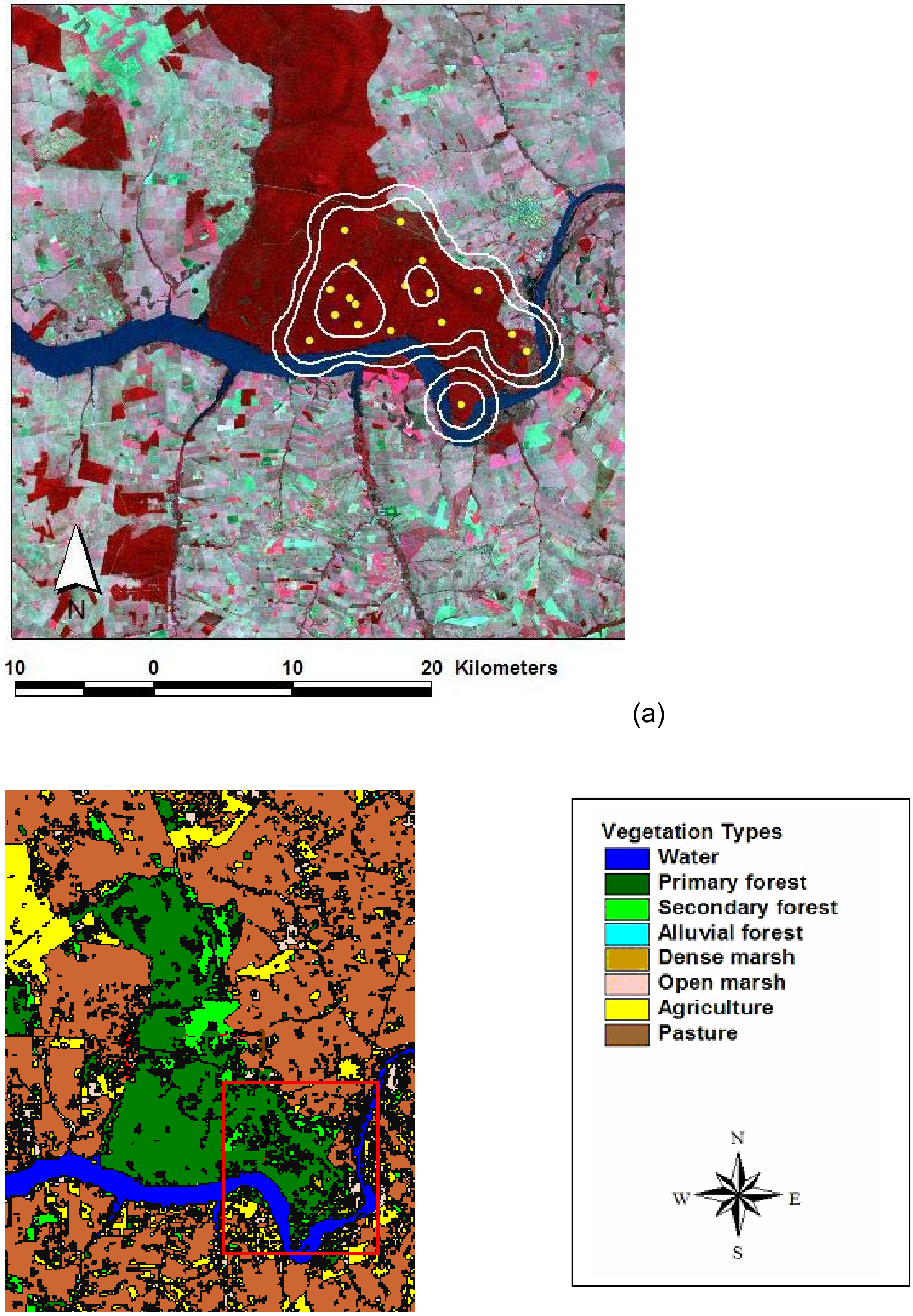


Figure 5.6. a) Dry 50, 85 and 95% fixed kernel home ranges and locations of adult F5 in the Morro do Diabo State Park. Home ranges were estimated using only 18 locations from the dry season.

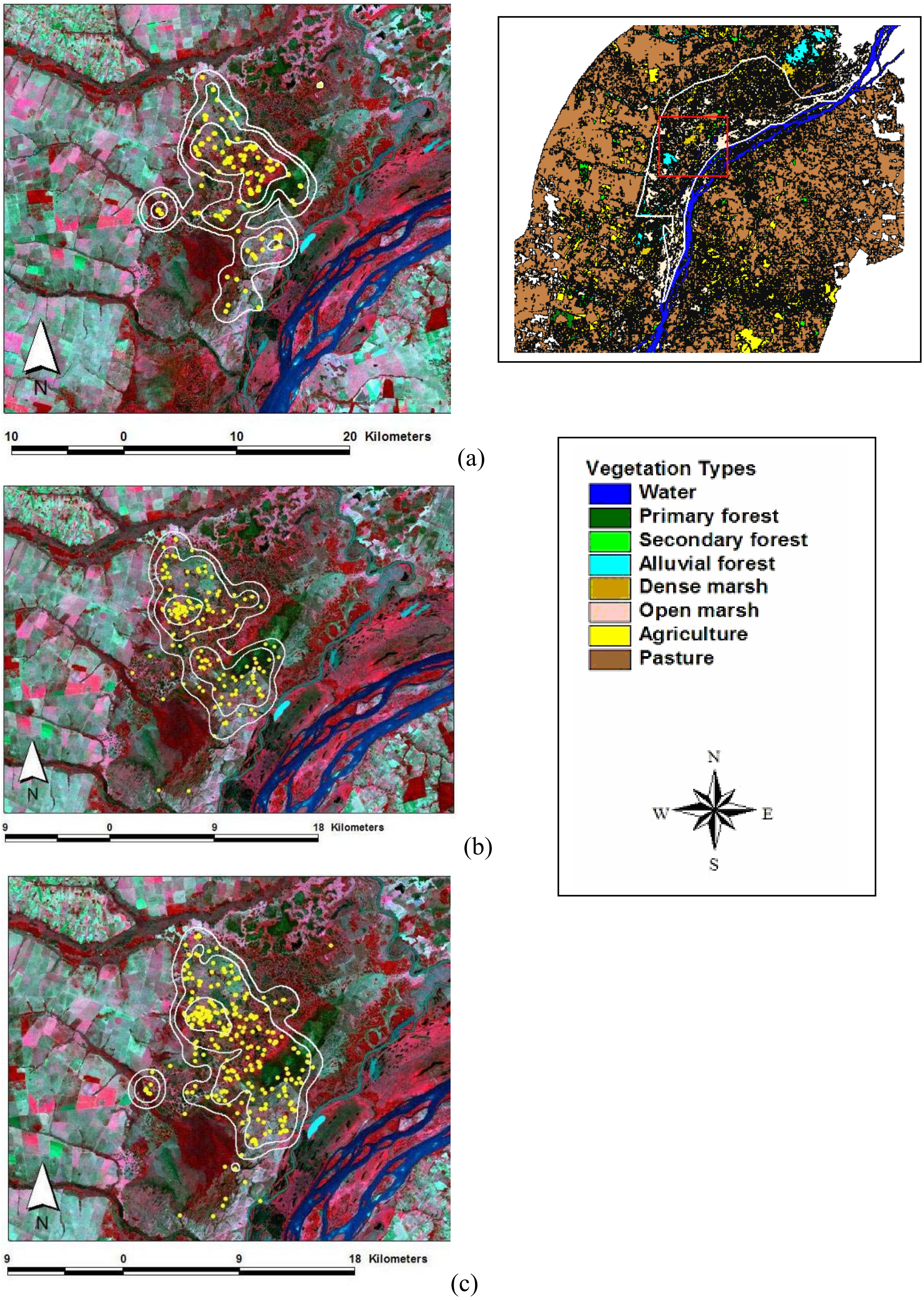


Figure 5.7. a) Dry season, b) wet season and c) annual 50, 85 and 95% fixed kernel home ranges and locations of adult F6 in the Ivinhema State Park. In the right figure, the white line demarks the limits of the State Park.

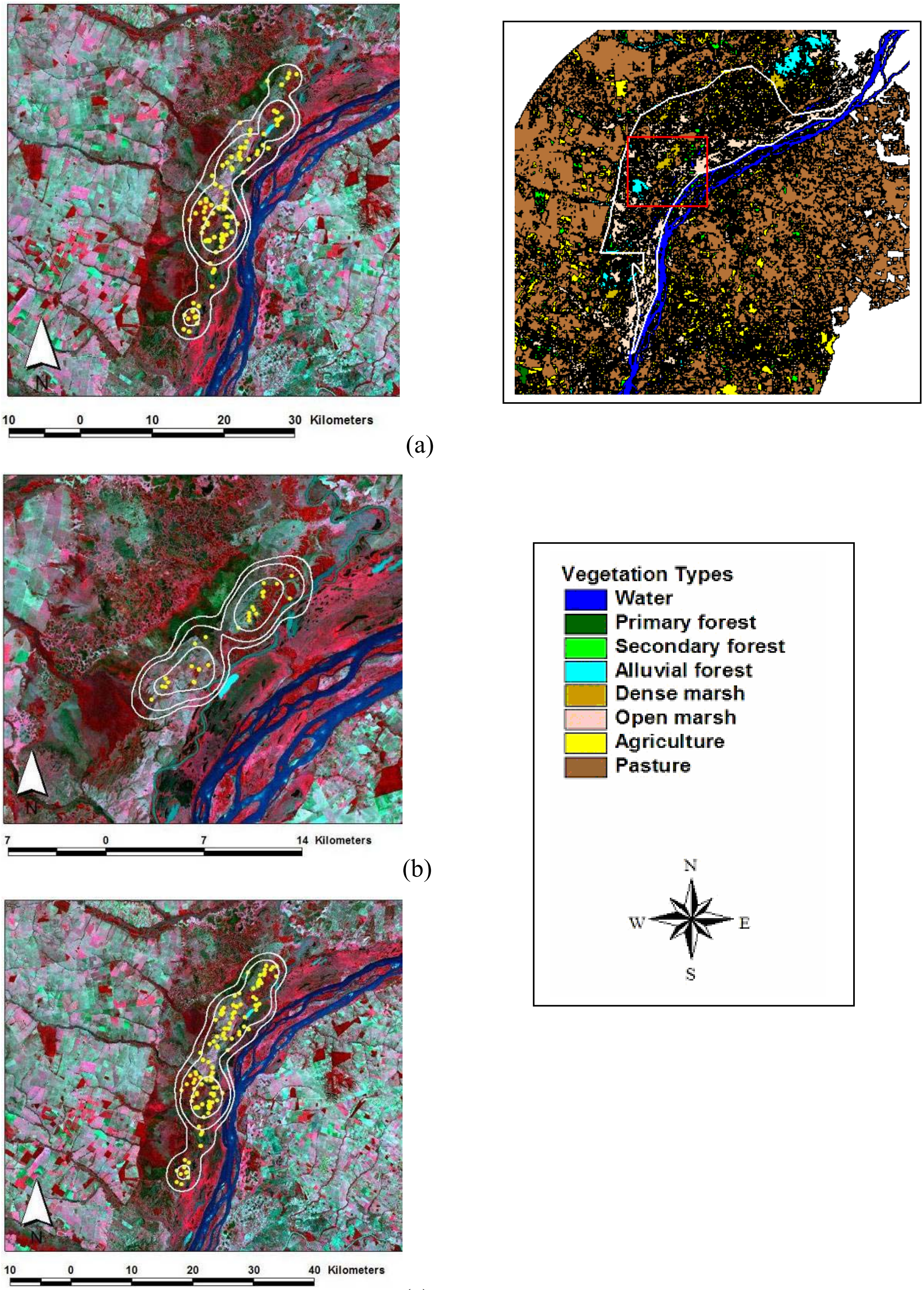


Figure 5.8. a) Dry season, b) wet season and c) annual 50, 85 and 95% fixed kernel home ranges and locations of adult F7 in the Ivinhema State Park.

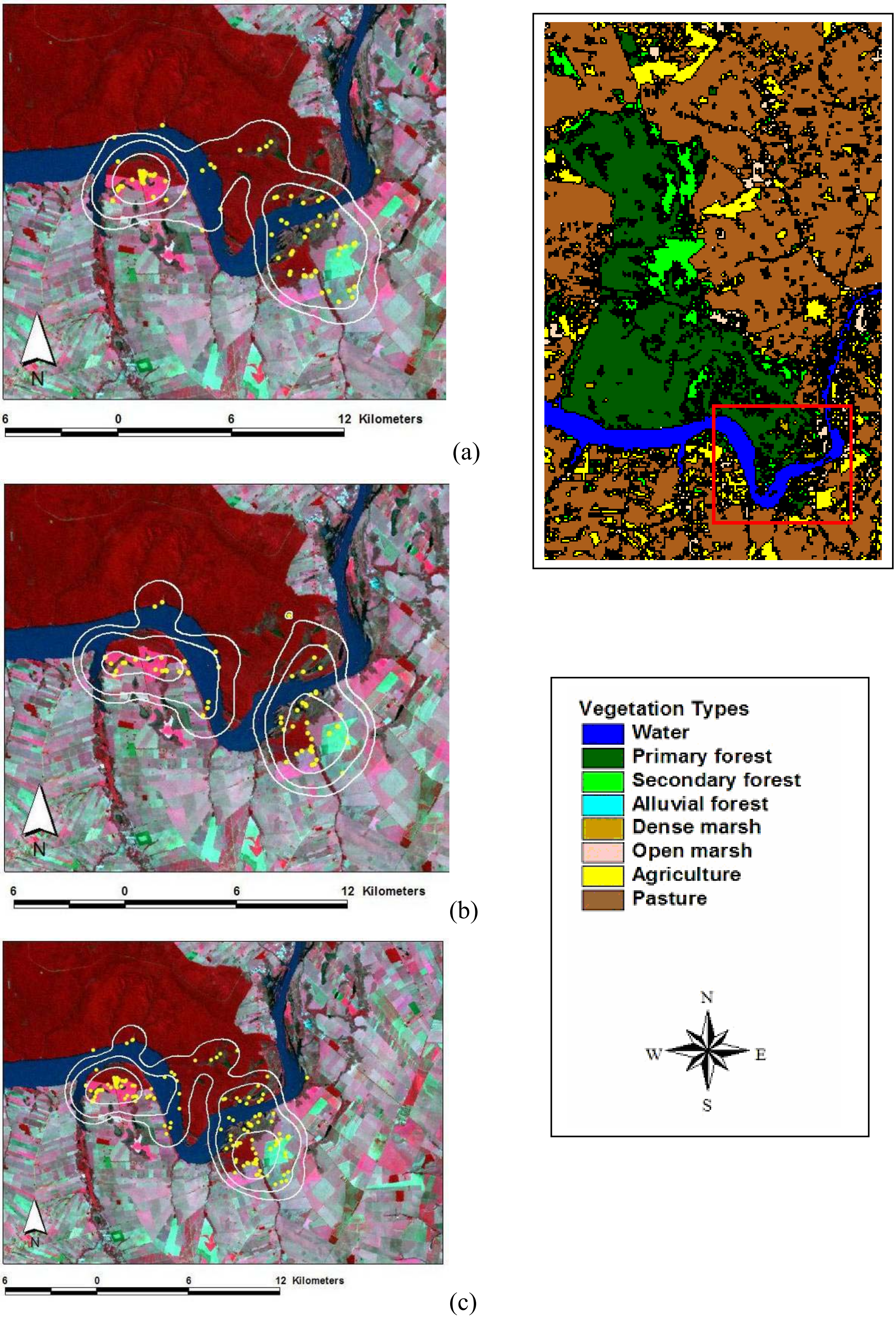


Figure 5.9. a) Dry season, b) wet season and c) annual 50, 85 and 95% fixed kernel home ranges and locations of adult M1 in the Morro do Diabo State Park.

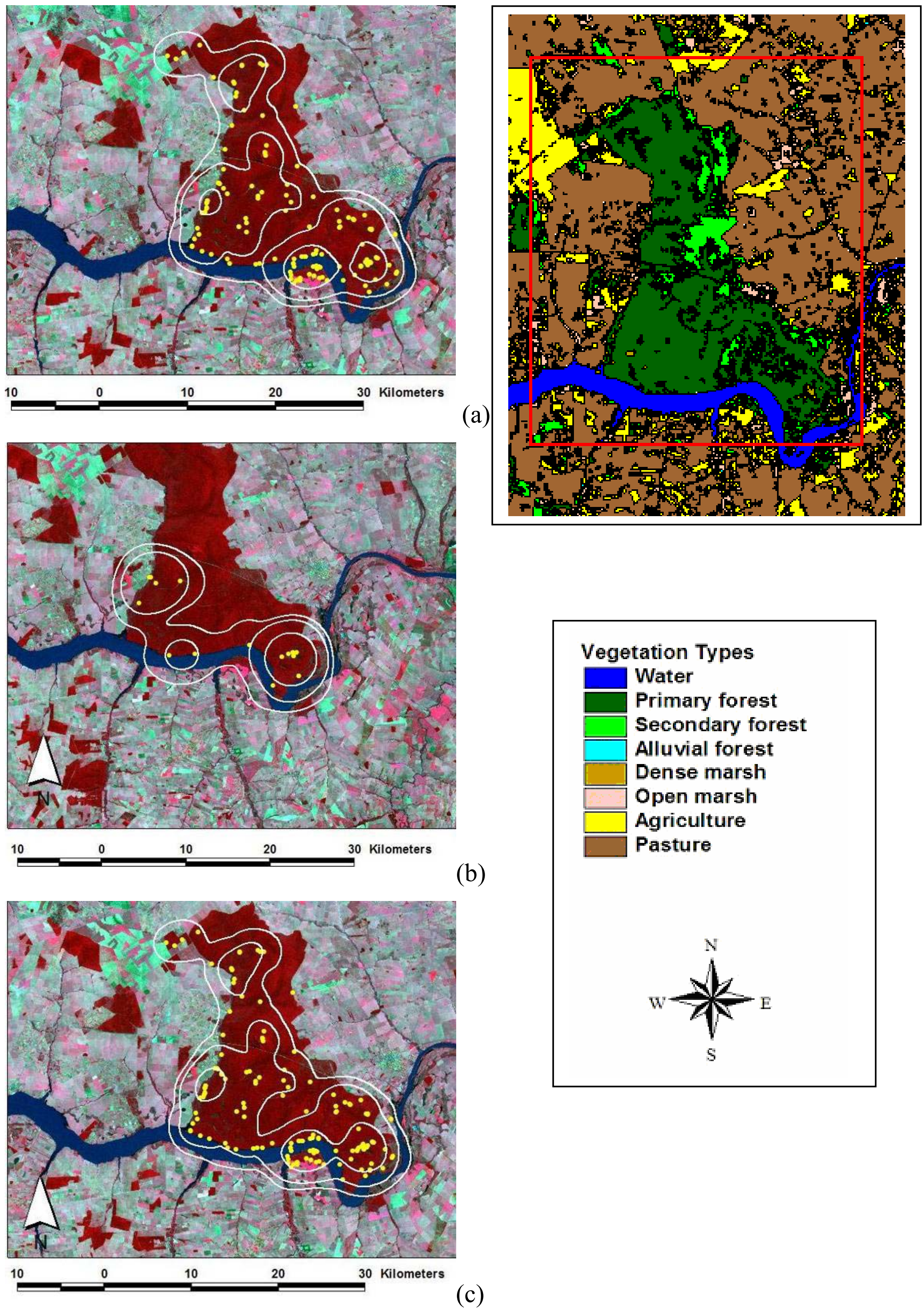


Figure 5.10. a) Dry season, b) wet season and c) annual 50, 85 and 95% fixed kernel home ranges and locations of adult M2 in the Morro do Diabo State Park.

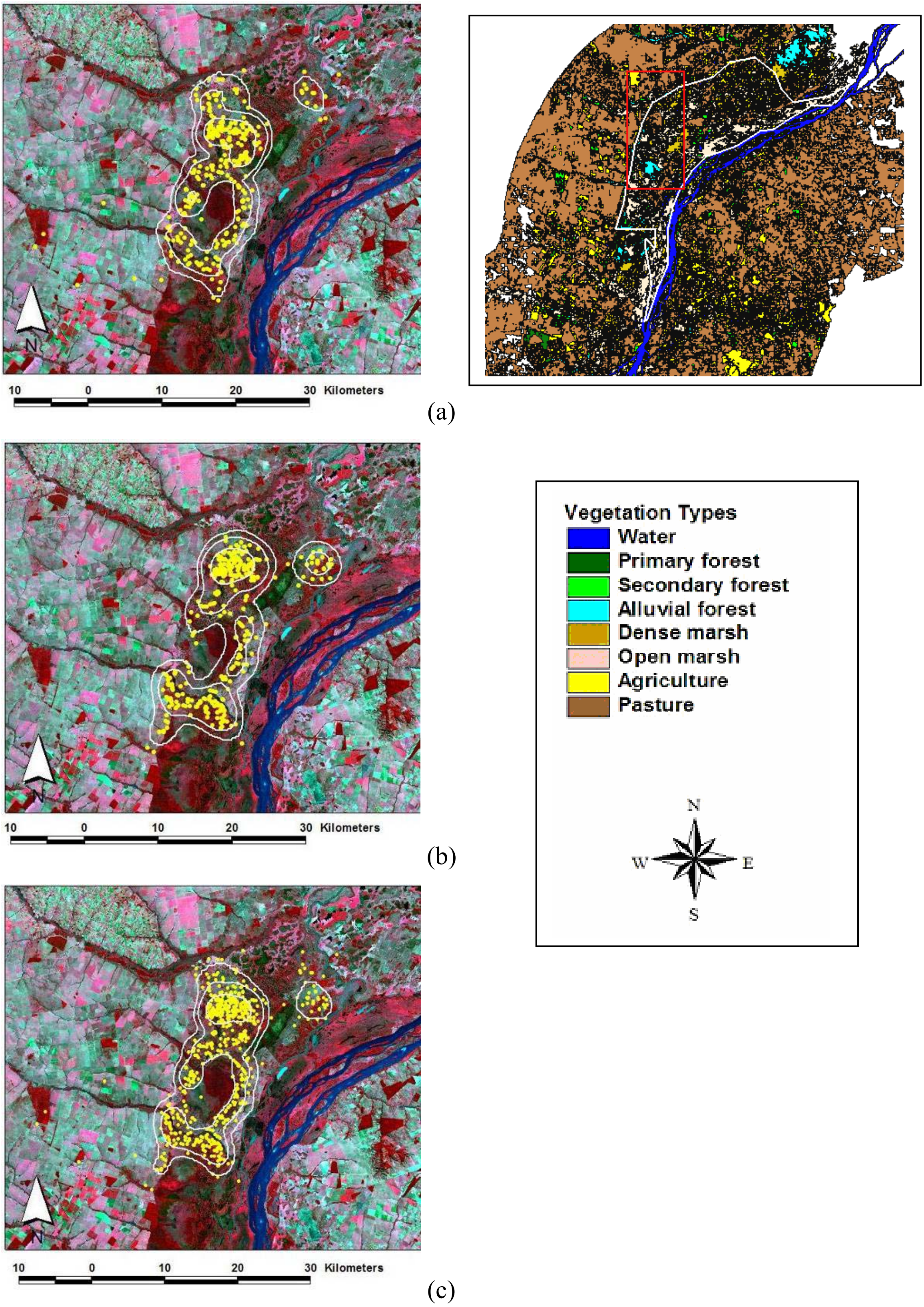


Figure 5.11. a) Dry season, b) wet season and c) annual 50, 85 and 95% fixed kernel home ranges and locations of adult M3 in the Ivinhema State Park.

5.3.3 Movements

The mean yearly straight-line distance between consecutive locations for all 10 individuals studied averaged 2.76 km (n = 2002, range = 1.11–5.88 km; Table 4.2). There were no differences in distances jaguars moved between consecutive locations in the wet season (2.85 km, SD=2.17) than in the dry season (2.40 km, SD= 1.83) (*T* test, P> 0.05). The maximum annual distance moved by all jaguars between consecutive locations averaged 13.18 km. The average maximum distance moved by jaguars between consecutive locations in the wet season (10.42 km, SD=5.76) was similar when compared to the dry season (10.23 km, SD= 5.33). Males and females moved similar distances between consecutive locations (Males = 3.13 km, Females = 2.49, *T* test, P > 0.05).

The VHF monitored Male 1 in Morro do Diabo moved the largest maximum distance between consecutive locations (20.46 km, Figure 5.11). His movements ranged over 95% of Morro do Diabo and included two forest fragments on the southern edge of Morro do Diabo. In addition, Male 1 frequently crossed the 2 km wide Paranapanema River, and moved to 400 ha forest fragment on the privately owned Copacabana Ranch.

In Ivinhema State Male 3 also moved a considerable maximum distance of 18.16 km between consecutive locations (Figure 5.12). GPS telemetry indicated that movements of over 15 km were not uncommon. Male 3 moved from Ivinhema to a 2.000 ha isolated forest fragment 30 km to the west. Again, GPS telemetry showed that this move required this adult male to traverse open pastures and gallery forests and was made in 3-4 days.

Table 5.2. Straight-line distances moved between of GPS and VHF radio-collared jaguars in the Upper Paraná River.

Individuals	Telemetry Type	Mean Distanced Moved (Km)			Maximum Distance Moved (Km)		
		Yearly (n)	Dry (n)	Wet (n)	Yearly (n)	Dry (n)	Wet (n)
		Morro do Diabo State Park					
M1	GPS	5.22 (156)	5.22 (138)	4.51 (18)	20.46 (156)	20.46 (138)	15.10 (18)
M2	GPS	2.50 (162)	2.48 (88)	2.49 (74)	12.36 (162)	11.19 (88)	12.36 (74)
F1	GPS	1.11 (92)	1.02 (58)	1.30 (34)	4.98 (92)	3.47 (58)	4.98 (34)
F2	VHF	5.88 (17)	-	5.88 (17)	13.02 (17)	-	13.02 (17)
F3	GPS	4.77 (35)	3.53 (24)	6.89 (11)	17.00 (35)	12.29 (24)	17.06 (11)
F4	GPS	1.27 (214)	1.31 (131)	1.20 (83)	4.75 (214)	4.75 (131)	4.59 (83)
F5	VHF	4.46 (18)	4.46 (18)	-	11.97 (18)	11.97 (18)	-
Mean Male		**3.86**	**3.85**	**3.50**	**16.41**	**15.83**	**13.73**
Mean Femele		**3.50**	**2.58**	**3.88**	**9.54**	**8.12**	**9.90**
		Ivinhema State Park					
M3	GPS	2.41 (799)	2.17 (399)	2.68 (400)	18.16 (404)	13.13 (399)	18.16 (400)
F6	GPS	1.64 (326)	1.75 (148)	1.61 (179)	15.87 (326)	15.87 (148)	15.63 (179)
F7	GPS	1.31 (183)	1.27 (154)	1.10 (29)	13.26 (183)	9.17 (154)	3.32 (29)
Mean Male		**2.41**	**2.17**	**2.68**	**18.16**	**13.13**	**18.16**
Mean Female		**1.48**	**1.01**	**1.36**	**14.57**	**12.52**	**9.47**

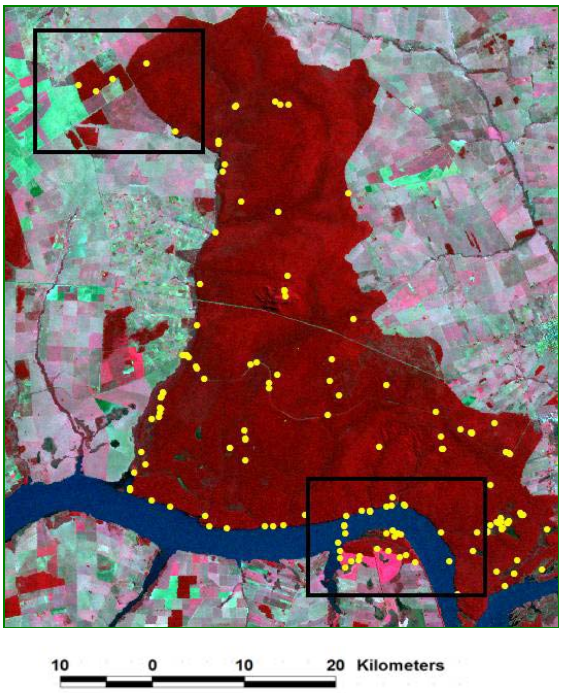


Figure 5.12. Movements of M1 adult male in the Morro do Diabo State Park, showing the use of a nearby fragment in the north and across the Paranapanema River to the south.

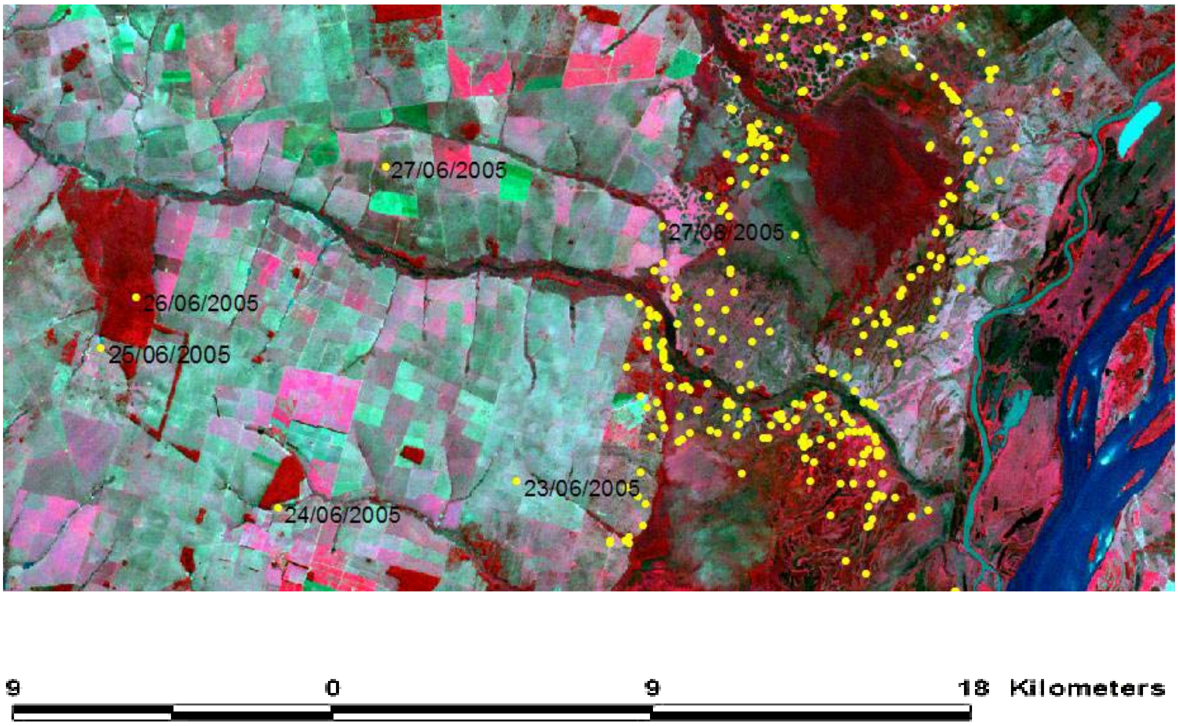


Figure 5.13. Adult male M3 moved outside the Ivinhema State Park to a 2000 ha isolated forest fragment 30 Km to west, using some gallery forests as travel routes. The dates associated with each location show that this movement required the adult male to traverse open pastures.

5.4 Discussion

5.4.1 Home Range Sizes

The home range size for jaguars reported in the literature is quite variable due both to differences in the estimation techniques used and in the environments studied. In Morro do Diabo, the yearly 85% home range averaged 162 km^2 (SD = 160) for male jaguars and 60 km^2 for females. In Ivinhema State Park, the only male monitored had a yearly 85% home range of 147 km^2, while that of the two females monitored averaged 130 km^2.

Male and female home ranges were larger for the jaguars studied in Ivinhema when compared to Morro do Diabo. Female home range in Ivinhema (n= 2) was approximately twice the size found for the females in Morro do Diabo (130 Km^2 versus 60 Km^2, respectively). Large home range size, lower density and small overlap are factors normally associated with low carrying capacity and low prey biomass. This association might explain the larger home range and the smaller overlaps observed for female jaguars in Ivinhema when compared to those of Morro do Diabo. Ivinhema was recently established, and most of its mosaic is still composed of abandoned and regenerating pastures. Recent camera trapping estimates in Ivinhema have shown a lower ungulate abundance compared with Morro do Diabo. Moreover, winter fires are common and might deplete jaguar prey and lower carrying capacity. For example, in August 2002 and again in February 2006 nearly 500 km^2 of Ivinhema was burnt or almost 65%, mostly in seasonally flooded marshlands and abandoned pasture.

In the Morro do Diabo, mean home range overlap was 25% for 4 pairs of neighbouring females. Overlap in the annual 85% home range of the 2 males averaged 32%. In Ivinhema the overlap in annual 85% home ranges with the two neighbouring adult females monitored was 15 %. I believe that the variation shown in jaguar overlaps is also related to edge/habitat effects, the availability of standing water, and the resulting variation in densities of the main prey species. Ivinhema has permanent sources of water and some associated forest cover. In Morro do Diabo there was a network of small water courses, but some were dry during much of the year, and permanent water was restricted to the Paranapanema River and a few larger streams. The movements of some study animals in Morro do Diabo followed some of these water courses. Furthermore, the homogeneous habitat and reduced availability of water may have influenced jaguar spacing patterns, resulting in a high degree of home range overlap.

The density of prey can influence the home range size of several vertebrate species (Davies and Houston 1984, Brown et. al. 1999), including for other species of the large cats (Karanth et al. 2004). Cullen et al. (2001) calculated an ungulate biomass of about 172 kg/ha in Morro do Diabo. Rabinowitz and Nottingham (1986) estimated a vertebrate biomass of about 210 kg/ha in Belize. The biomass of native vertebrates in the marshlands of Ivinhema is unknown, but is likely to be lower than that of Morro do Diabo, as evidenced by recent camera trap studies. For example, Schaller (1983) estimated a biomass of native vertebrates at 3.8 kg/ha in the Pantanal. With domestic stock (mostly cattle) included, that figure increased to 41 kg/ha. Using biomass as a general measure of prey availability (Kleiman and Eisenbeg 1973), the decreased prey availability would explain the larger home ranges in Ivinhema, when compared to Morro do Diabo and to Belize in Central America.

Crawshaw and Quigley (1991) showed that jaguar home range were larger during the dry season. In contrast, the results of this study showed no significant difference in jaguar home ranges between the seasons. Flooding in the wet season is the major ecological event in the protected marshes of the Upper Paraná River. The availability of dry land fluctuates with the water level. Much of the seasonally-flooded lowland savannas and seasonally-flooded semi-deciduous forests (alluvial forests) are under more than 1 m of water during the wet season. For most terrestrial mammals, this drastically reduces the effective area available for foraging. For example, averages of females jaguar annual home range in Ivinhema was 56 km^2 in the wet season and 107 km^2 in the dry season. In flooded habitat, the smaller home range size of jaguars during the wet season probably reflects the concentration of their food resource on the remaining higher ground. In the dry season, by contrast prey disperses and predators expand their home range.

The degree of flooding may also explain differences in home range differences between jaguars in Ivinhema and Morro do Diabo. Most of the Morro do Diabo is not affected by flooding. Thus, there was little change in the available land area for female jaguars during wet and dry seasons, making the differences in home range less pronounced (i.e. 91% difference in Ivinhema versus 35% in Morro do Diabo).

Previous studies on jaguar ecology have also reported that home range sizes for male jaguars were larger than those of females because of their polygynous breeding system (Table 5.3). In Morro do Diabo males had home ranges sizes about 3 times the size of females. Males M1 and M2 were the only adult males captured with camera traps and are presumed to be the only male residents in Morro do Diabo. The large size of their home ranges may reflect limited competition from other males in this isolated and fragmented area. These males covered about 380 km^2 (88%) of the study area with their combined annual 85% home ranges, and each consorted with between two-three females in the study area. The same trend in male home range size could not be observed in Ivinhema where the only collared male jaguar had a home range of 147 km^2, similar to the average reported for Morro do Diabo.

Table 5.3. Home range size for jaguars obtained using the 100% Minimum Convex Polygon in different studies in the Neotropics.

Home Range Size (km^2)		Habitat	Source	Country
Male (n)	Female (n)			
33.4 (4)	10.3 (3)	Forest	Rabinowitz and Nottingham (1986)	Belize
36.9 (2)	45.5 (2)	Forest	Ceballos et al. (2002)	México
88.7 (4)	70 (1)	Forest	Crawshaw (1995)	Brazil
90 (2)	32.3 (3)	Pantanal	Schaller and Crawshaw (1980)	Brazil
152.4 (1)	139.6 (4)	Pantanal	Crawshaw and Quigley (1991)	Brazil
130 (1)	49 (2)	Llanos	Scognamillo et al. (2002)	Venezuela
56 (7)	39 (2)	Forest	Crawshaw et al. (2004)	Brazil/Argentina
265 (2)	228 (1)	Cerrado	Silveira (2004)	Brazil
162 (2)	60 (5)	Forest	This Study *	Brazil
147 (1)	130 (2)	Marsh	This Study *	Brazil

* Home range estimates based on 85% Fixed Kernel

My estimates of jaguar home range size were generally larger than most reported in other jaguar studies in the Neotropics (Table 4.3). For example, using VHF radio telemetry, in Belize, Rabinowitz and Nottingham (1986), reported that home ranges of four males varied from 28-40 km^2, with a mean of 33.4 km^2. This figure is about three times smaller than the average home range for males in Morro do Diabo and Ivinhema. In the same study in Belize, two females had ranges of 10 and 11 km^2, respectively, or eight times smaller than that in Morro do Diabo. In contrast to my study, the home range of the two females did not overlap in Belize, but those of the males overlapped extensively. At Iguaçu National Park, in southern Brazil, home range estimates (Minimum Convex Polygon) varied considerably for the jaguars, ranging from 8.8 km^2 (female) to 138 km^2 (male) (Crawshaw et al. 2004). In the Brazilian Pantanal, the average home range size for 5 animals studied by Schaller and Crawshaw (1980) was 42 km^2. There are a number of possible explanations for these differences. Schaller and Crawshaw (1980) also worked in the marshlands of the Pantanal, but their study area was on the edge of the flood plain and less affected by flooding than Ivinhema. With more dry land year-round, prey and predator would require a smaller area in which to live so smaller home ranges might be expected. In addition to these differences, only 2 of 5 home range estimates made by Schaller and Crawshaw (1980) were made with the aid of radio-telemetry and none of their animals could be followed for more than 5 months.

The larger home ranges associated with lower jaguar densities in both of my study sites could also be attributed to the lower carrying capacities of semideciduous habitats. Both my study sites are bordered by the dry *Cerrado* vegetation. Morro do Diabo State Park is located right on the edge of the *Cerrado* and, accordingly, the best classification of Morro do Diabo forest would be an "upland semideciduous Atlantic Forest interspersed with some areas of Cerradão" (Baitello et al. 1988). In these habitats, primary production is lower and more erratic than in moister forests, while water availability is lower. This affects the distribution, density and biomass of prey species (Cullen et al. 2001). Silveira (2004) similarly reported large home areas for jaguars in the Cerrado of central Brazil, where average home range for males was 161 Km^2, very similar to my results for Morro do Diabo. The moist tropical forests and the alluvial marshlands of tropical South America, such as the "Llanos" in Venezuela and the "Pantanal" in Brazil, probably correspond to the Upper limit of jaguar densities, whereas the semideciduous habitats and *Cerrado* vegetation may correspond to the lower limits.

From a conservation perspective, this study supports the hypothesis that prey density is a key determinant of jaguar abundance. The results on home range size are consistent with the hypothesis that jaguar populations could decline because prey depletion caused by adverse human impacts. An understanding of the response of a jaguar population to long-term changes in prey biomass in terms of home range size and social structure could have important conservation implications. Indeed, home range size might be reduced by increasing prey density, and in turn increasing the density of the jaguar population. For example, Karanth (1991) suggests that by increasing prey density, more tigers can be “packed” into a given space.

5.4.2 Home Range, Movements and the Landscape Detectives

Conservation biologists are promoting the concept of metapopulation management, where isolated subpopulations should be managed to facilitate dispersal and allow gene flow (McCullough 1996; Noss et al. 1996; Haight et al. 1998; Mech and Hallett 2001, Wikramanayake et al. 2002). The basic idea is to protect the breeding populations as source pools while providing dispersal opportunities and maintain a larger population by managing strategic habitat patches in the landscape mosaic. Pulliam (1988) showed that as little as 10% of the metapopulation located in a refuge can act as a source and maintain the other 90% of the population distributed elsewhere, including in sink habitats.

Wide ranging movements and long dispersal distances are key attributes for landscape detective species and metapopulation conservation. Today, breeding jaguars are confined to protected areas in the Upper Paraná Atlantic Forest. Since jaguars can occupy large home ranges that can reach up to 470 km^2, the protected areas can support only a small proportion of a viable population. As a top carnivore, and with large home ranges, the jaguar should be a useful species for detecting and defining connectivity at coarse scales, between regions. In the long term, the jaguar will require inter-regional habitat linkages, for example, from the Iguaçu National Park in Brazil to Missiones in Argentina, in order to maintain viable populations (Cullen et al. 2004).

Long distance dispersal was not observed by any of the GPS collared individuals in this study. However, adult jaguars showed long distance movements within their home range, of up to 30 km in 3-4 days. They also moved through gallery forests as travel routes, and showed the ability to traverse long distances in open pastures and to cross relatively wide rivers. These life history and behavioural features makes the jaguar a good landscape species for designing conservation landscapes and also to capture other important elements of biodiversity that are less space extensive (Coppolillo et al. 2004). For example, with this information, the landscape detective model can help to identify strategic transit refuges or stepping stones for dispersing jaguars that could improve the dispersal potential of corridors between the identified suitable habitat patches. Thus, using this model recommendations should be made for reserve land-management and corridor restoration in a human-dominated landscape. In the following chapter, I present this model as a useful tool that could be used in designing similar conservation landscapes for other endangered mega vertebrates.

5.4.3 Relationship with Humans

On several occasions I responded to complaints from neighbouring ranchers and small settlers concerning predators, particularly jaguars. I personally attended over 20 complaints, most of them coming from the Copacabana Farm, which is located right across the Paranapanema River, on the southern border of Morro do Diabo. Some of these cases involved considerable losses. For example, in 2004, 56 head of cattle were reported killed by jaguars around Morro do Diabo with an estimated loss at roughly U$ 8.400.

Most people attributed such increases in jaguar predation to an increase in the population of jaguars in Morro do Diabo. However, jaguars F1, F4 and M1 had established adult core home ranges outside the Morro do Diabo boundaries, in the nearby mosaic of marshlands and forest fragments. This indicates that there could still be some open spaces in the population. Other hypotheses can be postulated: (1) the presence of cattle right in the edge of Morro do Diabo, could attract already habituated jaguars to these “easy prey” areas; (2) with knowledge about the project and the establishment of other institutional environmental programs in the area, and the critical status of the species, more conscientious ranchers and small land settlers tended to report losses than to eliminate the animal.

If home range sizes reported in this study are representative of jaguars across protected and non protected forests and marshlands of the Upper Paraná River, their density and total population may be much lower than at other Neotropical sites. Large-scale movements and large home range sizes may be an adaptation to low prey densities that occur in many parts of this human-dominated landscape. Lower population densities and movements that take these cats across habitats offering little escape cover make jaguars more vulnerable. This coupled with dependence on a natural prey population that is coming under increasing pressure from poaching and from agriculture expansion and domestic stock grazing, would argue for more protective measures. Brazil has expanded its protected areas system in recent years, but much of the prime jaguar habitat in this green corridor of the Upper and lower Paraná Rivers remains unprotected. Furthermore, many existing reserves are too small to afford protection of jaguars whose ranges seem to exceed the size of the parks. Given the endangered status of this jaguar metapopulation, conservation planners from throughout jaguar range should consider the potential for large home range requirements that is indicated by this study.

Ultimately, the fate of the jaguar in the Upper Paraná River, for that matter, of any large predators constrained within relatively small, isolated protected areas remain in the hands of the people that live around these areas and coexist with these species. However, it is the responsibility of managing agencies to resolve local conflicts that are inevitable in the interface between the natural and the man-modified world.

Prey management should be considered an integral component of jaguar conservation. Prey density in one of the critical issues in the Upper Paraná River today due to intensive poaching (Cullen et. al. 2001). Biologists, conservation organizations, funding organizations and policy makers need to focus on this issue. Habitat needs protection at the local level for prey as much as for jaguars and needs to be managed. Habitat needs to become good for jaguar prey and responsible prey managements should be made worthwhile to local communities. The formula seems straightforward: 1) protect large blocks of habitat so that jaguar populations are demographically stable and genetically viable, (2) give local people a reason to not poach jaguars, and (3) give the local people an incentive to support higher populations of key prey species such as peccaries, deer, tapirs, capybaras, mash deer. If prey species are abundant and poaching is minimized, the landscape will support jaguars over the long term. Only through the integration of applied research, implementation of management recommendations derived from these findings, involvement of NGO and Universities, co-management of protected areas, participation of local communities through community-based landscape restoration program, agroforestry extension and environmental education program, will these species have a chance to survive.

CHAPTER 6

JAGUAR HABITAT SELECTION IN THE UPPER PARANÁ RIVER, BRAZIL.

6.1 Introduction

In Brazil, quantitative information on habitat selection of jaguars living in semideciduous Atlantic Forest habitats has lagged behind studies conducted in tropical moist forests. The once extensive jaguar habitat of the semideciduous Atlantic Forest has been drastically fragmented and degraded, and today only about 8% of the natural habitat remains. An understanding of their habitat selection is relevant to managing the impact of hunting and trapping of jaguars, jaguar attacks on cattle stock (Crawshaw 2004), the impacts of habitat fragmentation (Cullen et. al. 2005) and for developing habitat suitability models for large scale conservation (Akçakaya 2004).

A number of previous studies have emphasized the importance of the area, landscape patterns and habitat selection in species conservation (Cantero et al. 1999, Estades and Temple 1999, Coppolilli et al. 2004, Haines et al. 2006). Large carnivore species such as the jaguar may require more than just large areas for their survival. Some species need certain habitat or vegetation types, and resources during their life cycle (Dunning et al. 1992, Mysterud et al. 2001). These required resources should be protected, as well as their configuration, to allow jaguars to establish their range and to move between habitat types. The Upper Paraná River is a very heterogeneous landscape and requires an evaluation of the composition of the landscape elements and how jaguars select among these different habitats. Habitat selection and specific requirements of the species is crucial to construct the landscape detective model. Species habitat requirements provided by habitat selection analysis are used with RAMAS-GIS software (Akçakaya 2002) to build a habitat suitability function in the model to define the landscape in which conservation must occur. I attempt to identify habitat patchiness from the jaguar’s perspective and to understand how the species perceives the patchiness of the landscape.

Although some aspects of jaguar ecology have been previously investigated across its range (Mondolfi and Hoogesteijn 1986, Bisbal 1989, Quigley and Crawshaw, 1992, Medellín et al. 2002, Crawshaw et al. 2004, Silveira, 2004), these researchers did not quantitatively assess habitat selection. Long-term studies on the species in Latin America have concentrated in home range analysis (Rabinowitz and Nottingham 1986, Crawshaw 1995, Crawshaw and Quigley 1991, Sana 2004), diet and prey base (Crawshaw 1995, Crawshaw et al. 2004, Polisar et. al. 2003, Weckel et al. 2006) and attacks on livestock (Polisar et. al. 2003, Cavalcanti 2004, Ordonez 2004).

In this chapter I used data from VHF and GPS radio-tagged jaguars to quantify how adult individuals in the Upper Paraná River region selected among the available vegetation types. I followed the framework developed by Johnson (1980) and Aebischer et al. (1993), in which animals make decisions about resource use at hierarchical stages, namely selection of home range within a study area (second-order selection) and selection of patches within a home range (third-order selection). First-order selection (selection of a species geographic range) was beyond the scope of this study. My main objective was to quantify habitat preferences at two orders of selection with respect to vegetation types and to test the null hypothesis that habitat utilization by jaguars was random at both study sites. This information was used to develop the landscape detective tool with a habitat suitability model and to link this model to a jaguar metapopulation viability analysis in the Upper Paraná River.

6.2 Methods

This study was carried out in the Morro do Diabo State Park in the State of São Paulo and in Ivinhema State Park State Park in the State of Mato Grosso do Sul. Detailed information about these two specific study sites is provided in Chapter 2.

6.2.1 Radiotelemetry and Habitat Selection

Between April 1998 and August 2005, 10 adult jaguars (> 2 years old) were captured, radio-collared, and monitored, 7 at Morro do Diabo State Park (MDSP) and 3 at Ivinhema, as discussed in Chapter 4.

I analyzed habitat selection separately for the dry season (April-September), the wet season (October-March), and for both periods combined. I use the term "annual" to indicate analysis using data pooled across >1 year of observation. A dry season includes locations for 2 or more dry seasons for a particular animal. All jaguar locations were plotted on a Landsat Satellite Image.

6.2.2 Compositional Analysis of Habitat Selection

Topographic map layers and habitat categories included variables most likely to explain jaguar spatial distribution. The term *habitat* was used as a layer of the proportions of a habitat class defined by vegetation type or other classifying factors and used by, or available to, an animal. Each habitat composition sums to 100%. To account for error in assigning an individual radio-location to a particular habitat type, the analysis assumed that a jaguar used all habitat types within a 100 m radius of a radio-location in proportion to the availability of habitat types within the circle (Figure 6.1). This study followed Rettie and McLoughlin (1999) who state that although the use of point data increases the probability of rejecting the null hypothesis of random habitat use, the use of point buffers will reduce the likelihood of drawing erroneous conclusions about relative preference. To evaluate second-order selection, I compared the habitat composition of the study area to the habitat composition of individual jaguar radio-locations. For third-order selection, I compared the habitat composition of an individual's yearly 85% home range to the habitat composition of the radio-locations of that individual during its yearly 85% home range.

At both scales of selection, I used compositional analysis to develop a ranking of habitat preference (Aitchison 1986, Aebischer and Robertson 1992, Aebischer et al. 1993). Compositional analysis uses the individual animal rather than the radio-location as the sampling unit, and avoids statistical problems arising from non-independence of proportions within a habitat composition (Aebischer et al. 1993). Because compositional analysis uses estimated habitat proportions rather than point data, the error and bias inherent in telemetry locations can be accommodated (Rettie and McLoughlin 1999).

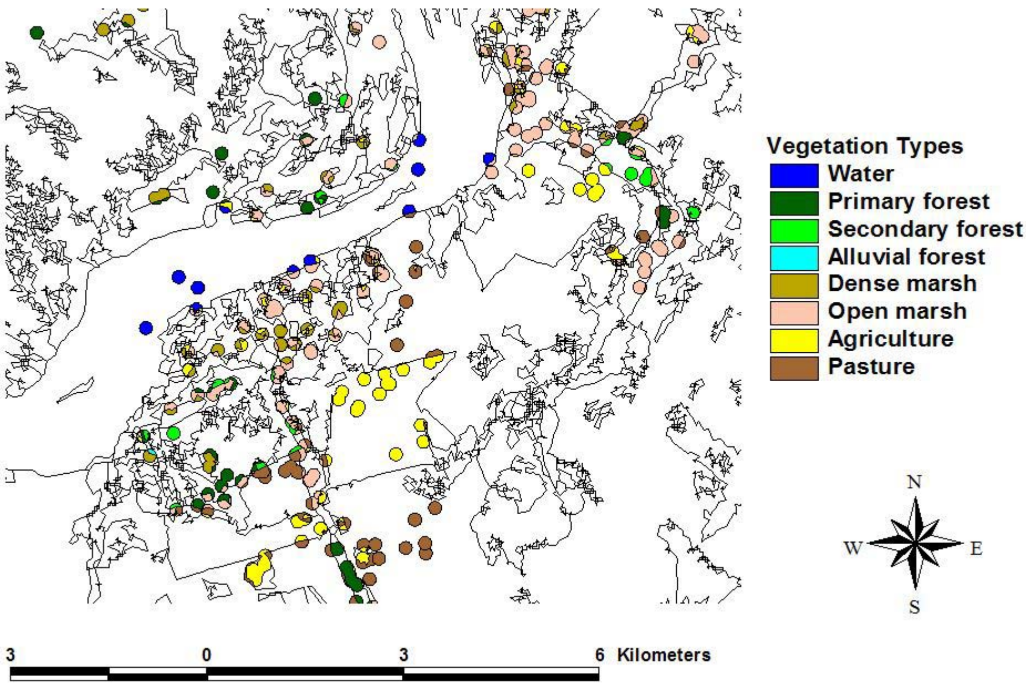


Figure 6.1. Habitat composition of individual, buffered jaguar radio-locations used to evaluate second and third order selection. Data are shown for Jaguar F4.

At both levels of analysis, I considered only those habitat classes available to all jaguars. Compositional analysis compares use of each habitat class to an arbitrary reference class k by the log-transformed ratio of habitat proportions for each animal (Aitchison 1986):

$$y_{ij} = \ln(x_{ij}/x_{ik}) \ (i = 1,\ldots, n;\ j = 1,\ldots,D;\ j \neq k)$$

where x_{ij} describes an individual i's proportional use of the j-th of D habitat types and n = number of individual animals. When an individual's proportional utilization of a habitat was 0, I replaced this value with a number less than one-tenth of the smallest observed value for that habitat (Aebischer et al. 1993). The differences between used and available habitat log-ratios for each individual formed a single row of a difference matrix with n rows and D-1 columns. To test the null hypothesis that utilization was random (difference matrix = 0), I constructed a residual matrix from the matrix of log-ratio differences and computed Wilk's lambda statistic, Δ , where:

$$\Delta = |R1| \ / \ |R2|$$

and where $R1$ is the matrix of mean corrected sums of squares and cross-products and $R2$ is the matrix of raw sums of squares and cross-product. Following the procedure proposed by Aebischer et al. (1993), I transformed Δ into the test statistic:

$$-N \ . \ \ln(\Delta)$$

which approximates a Chi-square distribution with k-1 degrees of freedom and where N is the number of individuals in the sample and k = the number of habitat classes. When habitat use was significantly non-random ($P < 0.05$), I calculated the mean and standard deviation for all log-ratio differences and constructed a matrix ranking of habitat types in their order of use. To assess differences between ranks, I used a paired t-test to compare mean utilization between all pairs of habitats.

6.2.3 Vegetation and Habitat Types

The vegetation cover of the Upper Paraná River region (including the MDSP and ISP) was analyzed digitally from 2002-2003 LandSat Images, using both ground knowledge and unsupervised classification of the three Landsat 7ETM satellite images that encompassed both study areas. The analysis was done with Erdas Imagine 8.4 and Arcview 3.3/Spatial Analyst. All vegetation types were categorized and classified. Initially, I identified 16 broad vegetation types and interpolated these across the two study areas. I further consolidated infrequent vegetation types into eight more general vegetation or habitat types (Tables 5.1 and 5.2, Figure 6.2). Lakes, rivers, and man-made watercourses were classified as water. Vegetation map layers and habitat categories included mainly those most likely to explain jaguar habitat selection and that composed the majority of the Upper Paraná River mosaic.

Table 6.1 Vegetation types in the Morro do Diabo Park study area used for habitat selection analysis by jaguar.

Vegetation Type	Total km^2	Proportional Habitat Availability
Water	110	5.33 %
Primary Forest	307	14.88 %
Secondary Forest	116	5.66 %
Alluvial Forest	1	0.05 %
Dense Marsh	25	1.25 %
Open Marsh	124	6.02 %
Agriculture	342	16.58 %
Pasture	1036	50.20 %
Totals	**2064**	**100.00 %**

Table 6.2. Vegetation types in the Ivinhema State Park study area used for habitat selection analysis by jaguar.

Vegetation Type	Total km^2	Proportional Habitat Availability
Water	186	5.28 %
Primary Forest	59	1.70 %
Secondary Forest	119	3.38 %
Alluvial Forest	80	2.29 %
Dense Marsh	153	4.34 %
Open Marsh	644	18.30 %
Agriculture	493	14.00 %
Pasture	1785	50.68 %
Totals	**3522**	**100.00 %**

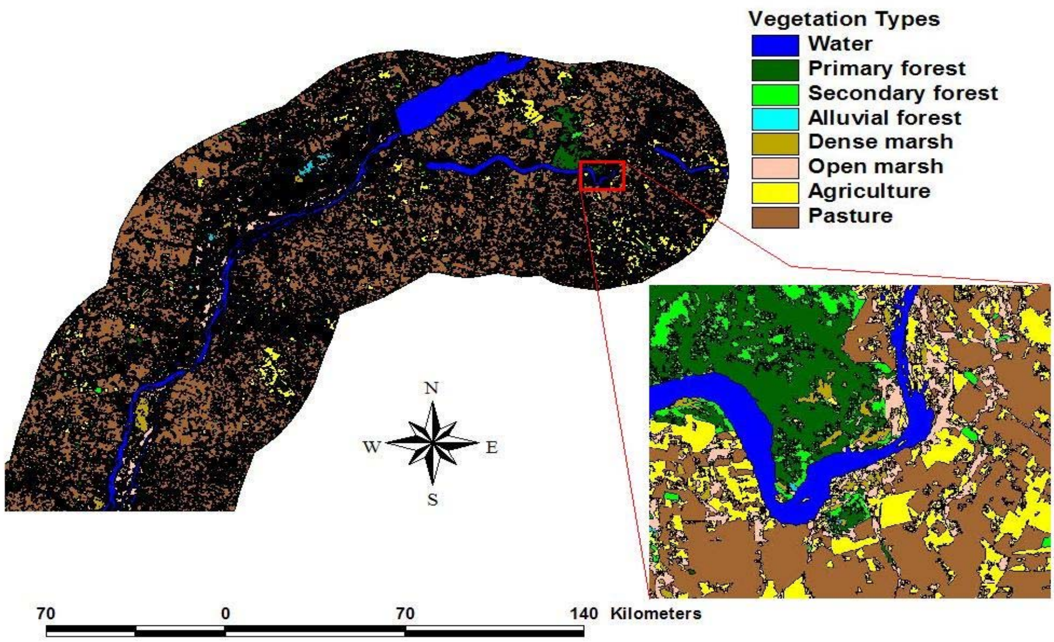


Figure 6.2. The 8 vegetation types used in the analysis of habitat selection by jaguars in the Upper Paraná River study area.

6.3 Results

6.3.1 Habitat Selection in Morro do Diabo State Park

Within the Morro do Diabo study area, the pre-dominant vegetation types were pasture (50%), agriculture (17%) and primary forest (15%). Open marshes and dense marshes were less dominant (6% and 1%), whereas alluvial forests were very rare (0.05%) (Table 6.3). In this area, jaguars selected dense marshes and primary forests and avoided human-dominated areas such as agriculture and pasture at both second-order scale, for radio-locations within the study area, and third-order scale, for radio locations within a home range (Figure 6.3, Appendix 1). At the second order, proportional use of vegetation types of the study area differs from habitat composition of the study area across seasons (Chi-square test, $P < 0.05$, n = 2 males and 5 females), and in the dry season ($P < 0.05$, n = 2 males and 5 females), but did not differ in the wet season ($P > 0.05$, n = 2 males and 3 females). Both within and across seasons, jaguars consistently preferred dense marshes and avoided disturbed areas. The rank order of vegetation types selected by jaguars varied slightly between seasons, as did the statistical significance of pairwise comparisons. Developed, disturbed, and agricultural vegetation types were consistently avoided.

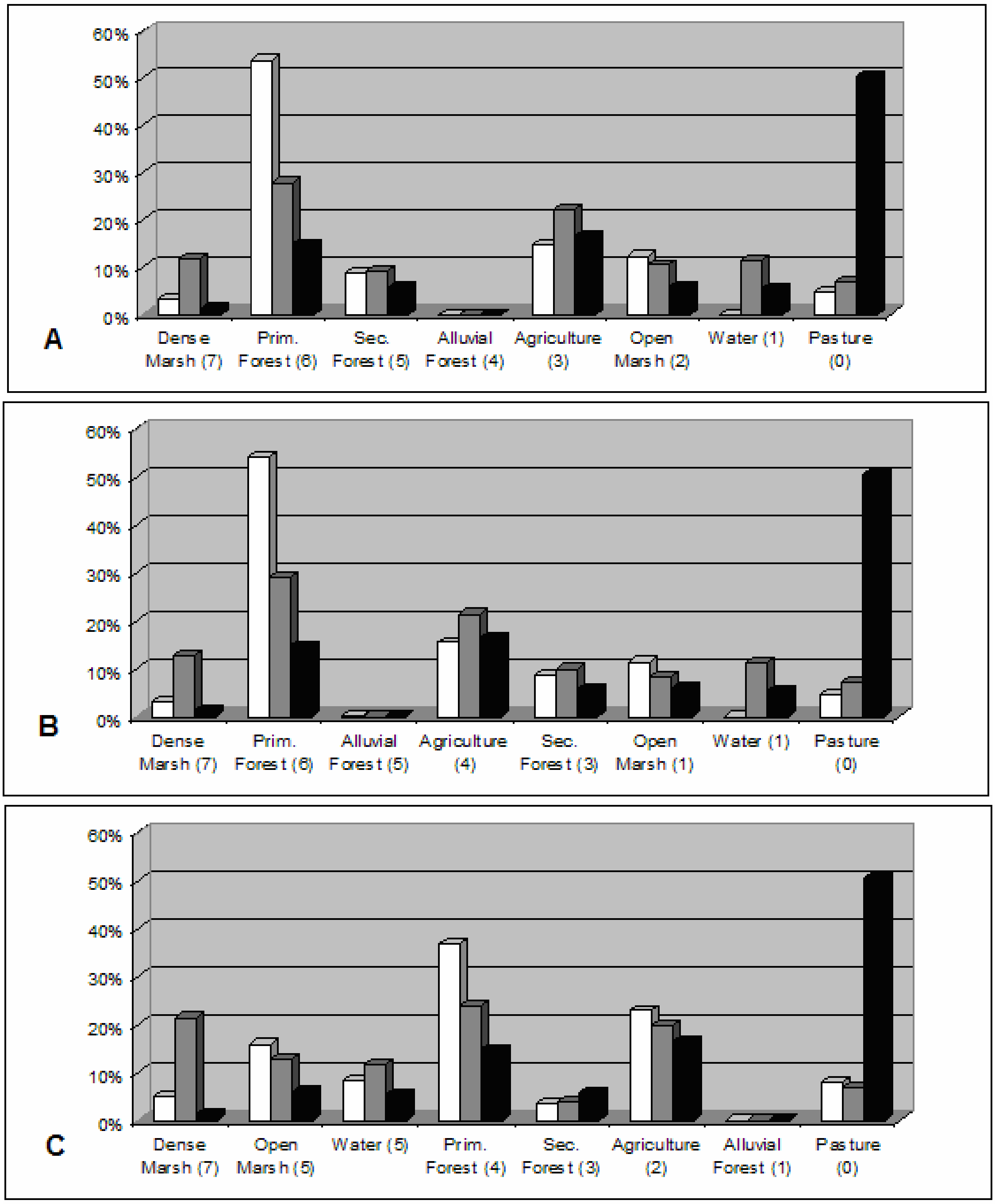
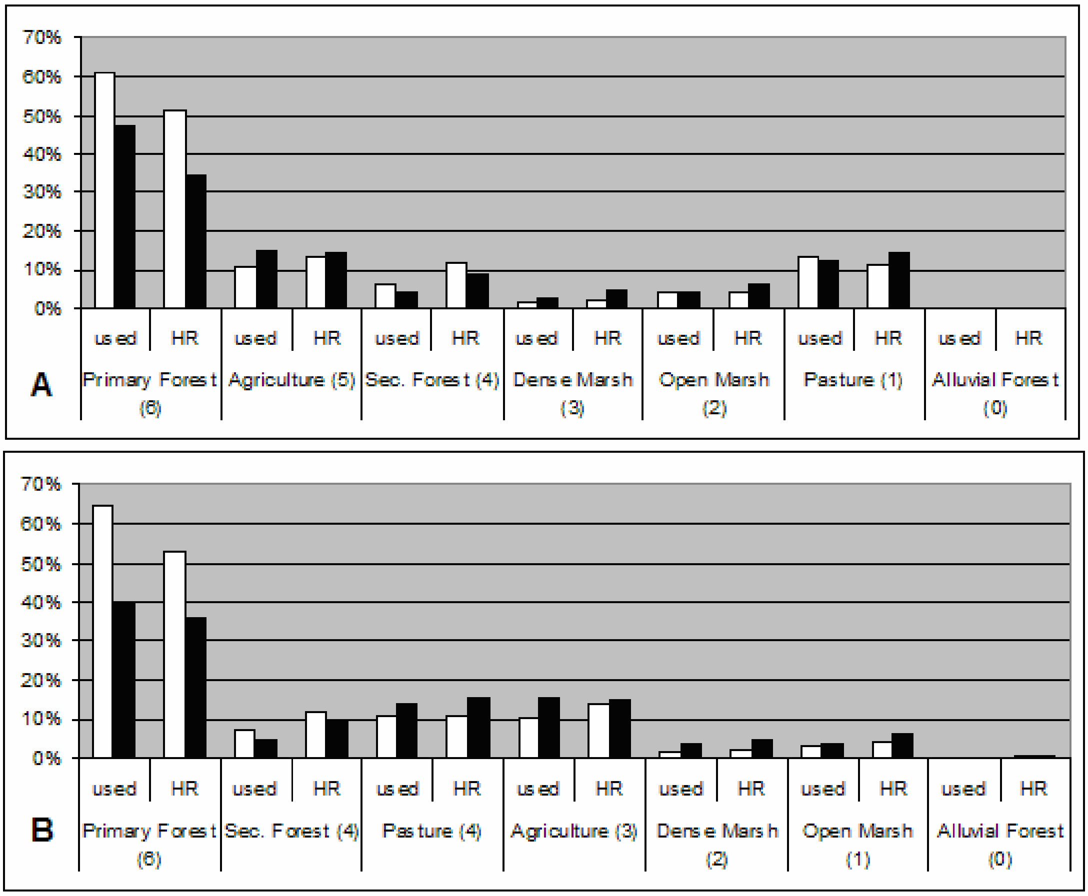


Figure 6.3. Second-order selection by jaguars in the Morro do Diabo study area. Vegetation types are arranged from most to least preferred for (A) seasons combined, (B) dry season, (C) wet season. White bars indicate mean female utilization, gray bars indicate mean male utilization, and black bars indicate habitat availability. Numbers of vegetation types on the x-axis indicate rank of preference for the vegetation types. In general, jaguars preferred dense marshes and primary forests and avoided pastures.

In assessing third-order selection, I eliminated the vegetation class "water" from the compositional analysis, because it was available to only a few individuals. For third-order selection, the habitat composition of an individual's yearly 85% home range (HR) was compared to the habitat composition of the radio locations of that individual captured in that yearly 85% home range. Use of vegetation types on multi-year 85% home ranges did not differ from availability in the dry season (Qui-square test *P* > 0.05, 2 males and 5 females), in the wet season (*P* > 0.05, 2 males and 3 females) and across seasons (*P* > 0.05, 2 males and 5 females) (Figure 6.4, Appendix 1). However, in all cases, primary forest was the most preferred habitat across all seasons. When pasture and alluvial forests occurred within a jaguar's home range, they were generally used in lower proportion than their spatial availability. At both orders of scale (second- and third-order), males and females were very consistent in their rank of preference of vegetation types.



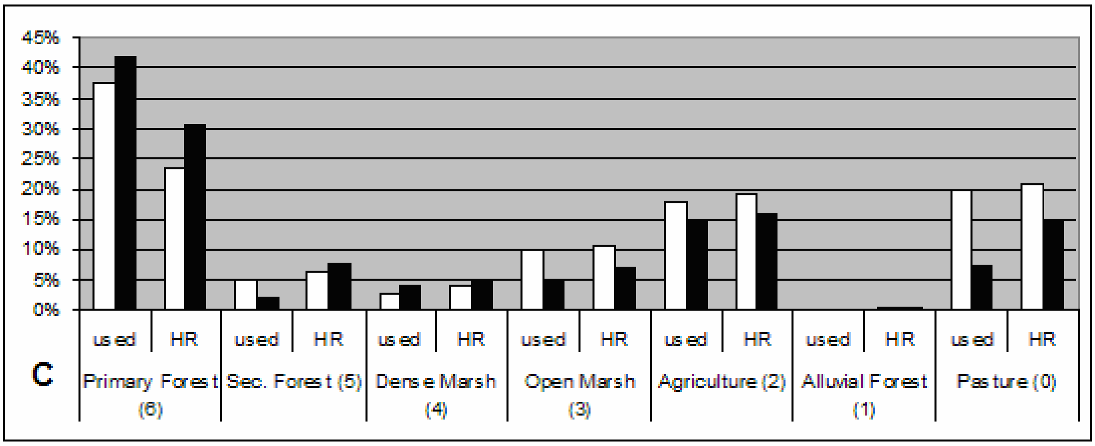


Figure 6.4 Third-order selection by jaguars in the Morro do Diabo study area. Vegetation types are arranged from most to least preferred for (A) seasons combined, (B) dry season, (C) wet season. White bars indicate mean female utilization; black bars indicate mean male utilization. Numbers of vegetation types on the x-axis indicate rank of preference vegetation. In general, jaguars preferred primary and secondary forests and avoided alluvial forests and pastures.

6.3.2 Habitat Selection in Ivinhema State Park

Within the Ivinhema study area, the dominant vegetation types were pasture (50%), open marsh (18%) and agriculture (14%). Dense marshes and secondary forests were less dominant (4% and 3%, respectively) whereas primary forests were very rare (1%) (Table 5.5, Appendix 1). In this area, jaguars selected dense marshes and open marshes and avoided primary forests at the second-order scale (radio-locations within the study area). At the second order, proportional use of vegetation types on the study area did not differ from habitat composition of the study area across seasons (Qui-square test $P > 0.05$, $n = 1$ male and 2 females), dry season ($P > 0.05$, $n = 1$ male and 2 females) and wet season ($P > 0.05$, $n = 1$ male and 2 females). Again, dense marsh was the most preferred habitat across all seasons. The rank order of vegetation types selected by jaguars varied slightly between seasons, as did the statistical significance of pairwise comparisons. Open water and primary forests were consistently avoided by jaguars.

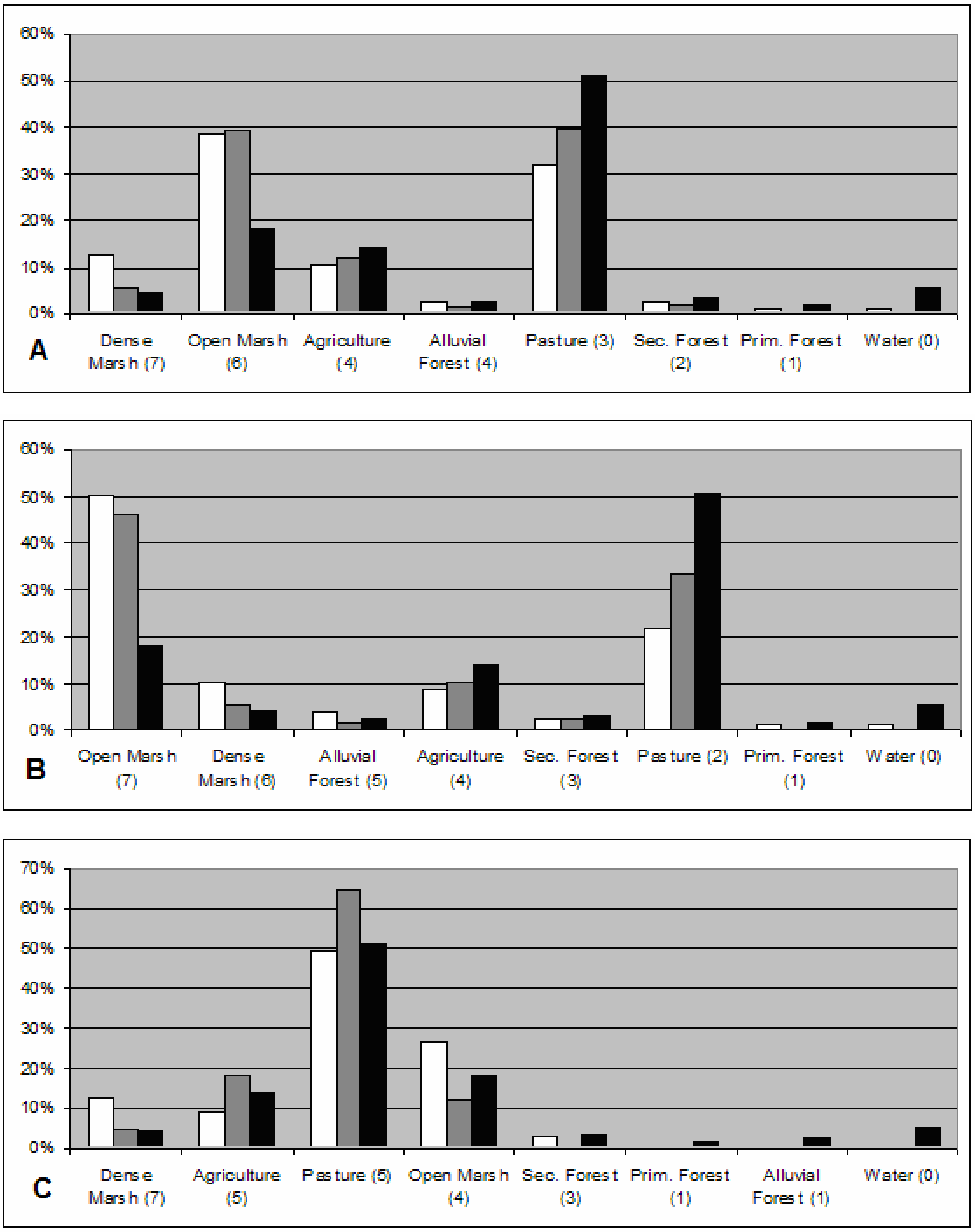
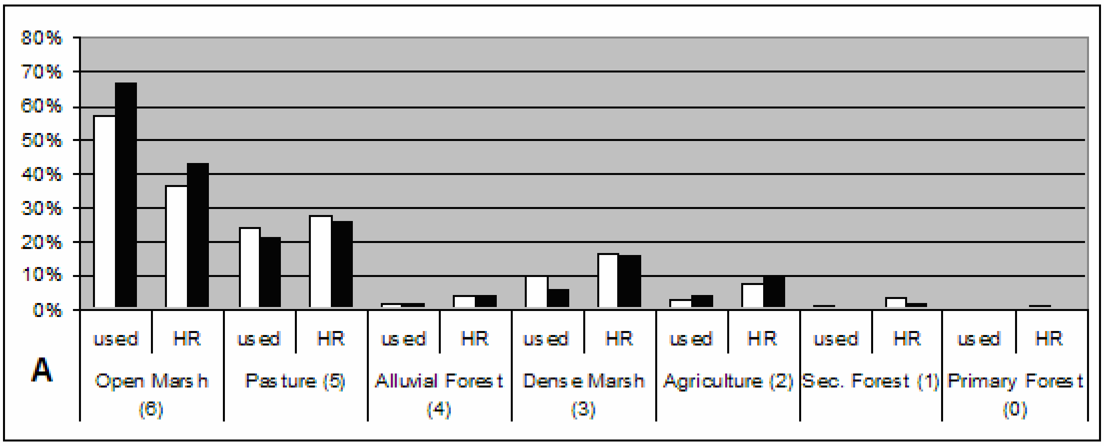


Figure 6.5. Second-order selection by jaguars in the Ivinhema study area. Vegetation types are arrayed from most to least preferred for (A) seasons combined, (B) dry season, (C) wet season. White bars indicate mean female utilization; gray bars indicate mean male utilization; and black bars indicate habitat availability. Numbers of vegetation types on the x-axis indicate rank of preference vegetation types. In general, jaguars preferred dense and open marshes and avoided primary and alluvial forests.

For third order scales, the use of vegetation types on multi-year 85% home ranges differed from availability across seasons ($P < 0.05$, 1 male and 2 females), but not for the wet season ($P > 0.05$, 1 male and 2 females) nor for the dry season ($P > 0.05$, 1 males and 2 females). Both within and across seasons, jaguars consistently preferred open marshes and abandoned pastures with some livestock maintenance, and avoided primary and secondary forests. The rank order of vegetation types selected by jaguars varied slightly between seasons as well as the statistical significance of pairwise comparisons (Figure 6.6, Appendix 1).



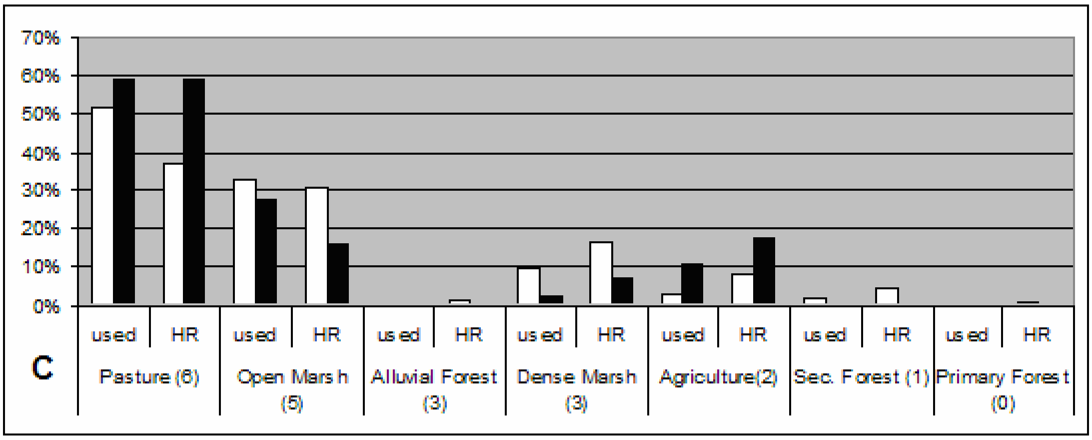


Figure 6.6. Third-order selection by jaguars in the Ivinhema study area. Vegetation types are arrayed from most to least preferred for (A) seasons combined, (B) dry season, (C) wet season. White bars indicate mean female utilization; black bars indicate mean male utilization. Numbers of vegetation types on the x-axis indicates rank of preference vegetation. In general, jaguars preferred open marshes and pastures and avoided primary and secondary.

6.4 Discussion

Few studies have investigated habitat selection of jaguars, and those that reported habitat use by jaguars have not documented habitat selection at the fine scale reported in this study, with the use of modern GPS telemetry. However, the habitats selected in this study were consistent with those documented elsewhere, in that jaguars show a strong affinity for dense and well watered lowlands and habitat edges. In this study, jaguars in general preferred dense marshes and avoided human-dominated areas such as intensively managed open pastures. In second and third-order scale, alluvial forests and pastures were consistently the most avoided vegetation type at both study sites. My results support findings by Logan and Irwin (1985), Laing (1988), and Williams et al. (1995) that significant avoidance of pastures and open vegetation areas by cougars is due to a lack of sufficient cover. Although the aversion to disturbed and developed habitat types by jaguars is not surprising, this study is the first to document such avoidance.

In the Morro do Diabo, where jaguars preferred forest habitat, the use of aquatic environments such as open water, dense and open marshes seemed to increase in the wet season, while the use of forested environments (primary forest and secondary forest) decreased. A similar trend was observed in the third order scale. In Ivinhema, jaguars significantly avoided forested environments, which occur in very low proportions. During the wet season, jaguars increasingly made use of higher elevations, apparently preferring dry and abandoned pastures with some livestock.

The close association of jaguars with water has long been described by naturalists and explorers (Roosevelt 1914, Miller 1930, Perry 1970). As reported in this study, the species shows a preference for terrain close to rivers, streams, and dense marshes (Cabrera and Yeppes 1960, Guggisberg 1975, Mondolfi and Hoogesteijn 1986, Bisbal 1989). Even when jaguars use open, dry areas, they always seek cover in nearby dense vegetation (Mondolfi and Hoogesteijn 1986, Rabinowitz 1986). As reported by Crawshaw and Quigley (1991) in the Miranda

Ranch in the Pantanal, jaguars were rarely found far from water and used dense marshlands and gallery forest more often than expected on the basis of their availability. In Morro do Diabo, the areas with lower prey abundance are those of dry open “cerrados” in the far north of the study area (Cullen et al. 2001). The same occurs for the dry pastures that are used for livestock in Ivinhema. These pastures are bordered by the dry forest, a habitat more frequently occupied by puma than jaguar (Sana 2004). This trend in habitat use by these species was also observed by Maxit (2001) in the Venezuelan Llanos, and in this study, from a single radio-collared puma in Morro do Diabo.

Contrary to earlier assessments, jaguars in the Upper Paraná region do not appear to be closely tied to forested environments (primary and secondary forests). This is specifically the case of jaguars living in the Ivinhema area where both types of forests were ranked very low in habitat preference. The distribution of semideciduous forests in this ecosystem has decreased dramatically due to repeated fires and intensive logging over the past century (Campos 2006). Jaguar distribution was probably more closely related to the dense forests prior to these disturbances. However, jaguars have thrived even since the Atlantic forests have been deforested, suggesting that jaguars are not solely dependent on dense forest types. Today, dense and open marshes that comprise only about 15% of the Upper Paraná landscape are the main habitats for the remaining jaguar populations.

In this study, dense marshes along riparian vegetation ranked first in use by the jaguar, but several other associated vegetation types were also important. The ecotones of vegetation types that create productive edges seem to be a key factor in defining desirable jaguar home ranges, both in Morro do Diabo and Ivinhema. Thus, the situation for the jaguar may be similar to that of the tiger, whose prey is most abundant where grasslands, dense marshlands and forests form a mosaic, and the interdigitation of many different vegetation types supports a rich ungulate community (Sunquist et al. 1999). This same situation was observed by Polisar et al. (2003) in the llanos of Venezuela, where prey abundance and jaguar habitat use was high in lowland dense marshlands and well-watered forest-savanna habitats. The attraction of other carnivores to prey-rich lowland forest-marshland ecotones has also been noted in other studies of sympatric species (Palomares et al. 1996, Durant 1998, Scognamillo et al. 2003).

In the Upper Paraná River, especially in the region of Ivinhema and Ilha Grande National Park, further to the south, the marsh deer (*Blastocerus dichotomus)*, is an important prey item in the jaguar diet (Oliveira 1992), and this species prefers riparian areas and dense marshes (Tiepolo 2002). In 2002, an aerial survey was conducted to estimate the population size and the abundance of marsh deer throughout the Upper Paraná River floodplain, using the double count method. The population was estimated as 1,079 ± 207 individuals for 1,081 km^2, which gives a density of 0.998 ± 0.192 deer/ km^2 and an estimated biomass of 120 kg/ km^2. This estimate is the highest reported for the species in Brazil (Schaller and Vasconcelos 1978, Mauro 1993, Mourão and Campos 1995, Pinder 1996, Tomas et. al 2002).

The use of dense marshes adjacent to riparian areas and forest patches probably enhances the jaguar’s ability to stalk and kill prey, including the marsh deer. In both Morro do Diabo and Ivinhema, these ecotones should provide good stalking cover and ambush sites (vegetation height typically < 1.5m). Riparian areas in major drainages should also provide important movement corridors for jaguars, associated with travel paths, as indicated by the home range of jaguars in Morro do Diabo (Chapter 5). Undoubtedly, the dense marshes bordered by the riparian areas provide important stalking and feeding cover for the Upper Paraná River jaguar populations, as kill sites and caches were most often associated with this vegetation type.

The second and third-order selection of jaguar should correspond to selection of habitat parameters that normally relate to prey distribution. At the third order scale, an animal should attempt to include within its home range those parameters that increase the potential for reproductive success. Indeed, jaguars in both Morro do Diabo and Ivinhema, at third order scale seemed to select home range locations that corresponded with habitat types that differed from the second order scales. At the third order selection the core areas of jaguars was where prey seemed to be more abundant. For example, in Morro do Diabo area, jaguars select marshlands at the second order selection and primary forests at third order, where ungulate density is high (Cullen 2001). In Ivinhema, jaguar select dense and open marshes at the second order, and upland areas such as pastures at the third order, where cattle ranching and calving was intense. Our field reports also support this evidence where cattle predation by jaguars seemed to increase in the wet season in Ivinhema State Park when jaguars increasingly made use of higher elevations, apparently preferring dry and abandoned pastures with some livestock for prey. The movements to higher elevations in the wet season is also explained by the inundation in the lowland areas with higher precipitation. These results have important management implications. For example, efforts in field monitoring and farmer outreach should be prioritized in the rainy season, because in the rainy season jaguars concentrate their range in higher areas where farmers have cattle. In these areas, in the rainy season cattle predation by jaguars will increase and conflicts with land owners may emerge.

6.4.1 Habitat Selection and Landscape Detectives

Jaguars showed preference for dense and open marshes in these study areas and this has important implications for the landscape detective approach. Combined, dense and open marshes still comprise approximately 15% of analyzed landscape. These marshes are the only potential jaguar habitats that continuously connect the remaining protected areas along the Paraná River basin. Marshes are still in good conditions along the Paranapanema River, downwards to the Paraná River, connecting the Morro do Diabo to the Ivinhema State Park, and Ivinhema to other protected areas nearby (Campos 2004). These productive marshlands may facilitate natural dispersal and allow genetic exchange among jaguar subpopulations. As marshlands are among the habitats preferred by jaguars, and connectivity is needed for the metapopulation conservation (Hanki and Simberloff

1996) my results seems to support that jaguars might be a good candidate for landscape species in this region.

The habitat selection indicates that the jaguar populations that appear to be fragmented and isolated could be linked by their preferred habitats, revealing the existence of potential marshland corridors and habitat linkages that were not readily apparent. In a simulation of cougar populations, Beier (1993) showed that immigration into a small population of one to four animals during a decade can significantly increase persistence. Similarly, persistence of jaguar populations in the Upper Paraná River can be enhanced if these populations can be managed as a metapopulation. Maintaining these habitats before they become totally converted is important for landscape conservation and jaguar metapopulation management.

When third order selection is analyzed, the core areas of jaguars was upland and pasture, where private cattle ranching is intense. In these areas, conflicts with farmers are common because of cattle predation. The long-term survival of jaguar subpopulations is dependent on the movement of dispersing jaguars between habitat patches. If dispersal is hampered, because of jaguars become established in these “low quality and dangerous sinks” subpopulations, they can suffer high probabilities of extinction, from genetic, demographic, or environmental stochasticity or catastrophes in small patches (Shaffer 1987). Conflict with farmers and poaching of jaguars from local populations could contribute to a source-sink structure (Hanski and Simberloff 1997), and destabilize the metapopulation. In sum, jaguars seem to have the ability to survive and to disperse in marshland habitats. However, their fate could be negatively influenced by frustrated establishment and dispersal in cattle ranching environments owned and managed by conservation unfriendly people. Key private inholdings used and identified by these jaguars need to be protected and take full consideration of further conservation measures.

Management of a healthy population of jaguars in the Upper Paraná River must also focus in maintaining the native marshland community. Large patches of dense and open marshlands interspersed with primary and secondary forests harbour sizeble populations important prey items of jaguar such as capybaras, peccaries and marsh deer. My results demonstrate that jaguars forage in areas without marshlands less than expected based on availability. Jaguars were especially dependent upon marshland habitats even when these habitats were rare in the landscape, as demonstrated for the Morro do Diabo region. In managing the remaining landscape I recommend that habitat alteration should not reduce the size of marshland patches below the mean jaguar home range observed in this study with observed yearly 95% home ranges of 18-471 km^2. Marshland and forest parches larger than this should also provide space and habitat for vagrant and dispersing jaguars in this highly fragmented landscape. One of the most important findings that emerge from this study is the importance of the marshlands as critical habitat for jaguars. The Upper Paraná River has already lost over 60% of its open and dense marshlands due to the impacts of drainage projects for rice plantations, cattle ranching and hydroelectric dams (Campos 2006). If the small protected areas, such as the ones already existing in the Upper Paraná region are to sustain jaguar populations they must include and protect as much of these marshlands as possible, so that jaguars can disperse, hunt wild prey and rear their cubs undisturbed. What is urgently needed in these jaguar conservation units is the creation of more large protected areas that can sustain jaguars in their favoured habitat.

CHAPTER 7

JAGUARS AS LANDSCAPE DETECTIVES AND A HABITAT-BASED POPULATION VIABILITY ANALYSIS FOR THE UPPER PARANÁ RIVER

7.1 Introduction

A landscape-scale approach to nature conservation calls for large, connected core areas with their full complement of native species (Soulé and Noss 1998). The central goal of this approach is to maintain or restore ecologically viable populations of large carnivores and other keystone species (Soulé and Terborgh 1999, Foreman and Daly 2000, Steneck 2005). Remaining jaguar (*Panthera onca*) populations are becoming increasingly fragmented and isolated throughout the species' range. In the Upper Paraná River, in the Brazilian Atlantic Forest region, the jaguar may exhibit a metapopulation structure, and an important step in assessing the status of jaguars is to determine the its structure in this region. A metapopulation is a group of geographically related sub-populations. Its structure is the number, size, spatial configuration and degree of isolation among these sub-populations (Hanki and Simberloff 1996). To describe the metapopulation structure of large carnivores requires information on where they live in relation to the size and spatial pattern of habitat types, where barriers exist that separate breeding populations (Smith et al. 1987, Ahearn et al. 1990, Smith 1993) and where habitat is degraded.

The Upper Paraná River provides a unique opportunity to study jaguars as landscape detectives. I define landscape detective as organisms that can show us how to plan and manage reserves and large interconnected eco-regions, because their requirements for survival require maintaining ecologically healthy habitats. Within the western Atlantic Forest range, the Pontal do Paranapanema region, together with the Upper Rio Paraná ecosystem still maintains approximately 50.000 km^2 of relatively semi-connected and well-preserved semideciduous

Atlantic Forests and marshlands. It is considered among the few areas where large carnivores such as jaguars, pumas and ocelots might persist (Sandenson et al. 2002).

Effective conservation and management strategies for endangered species such as jaguars relies on the integration of data and insights from diverse fields of investigation, leading to an understanding of past and present patterns of population dynamics, and an ability to project their population trends in the future (Eizirik et al. 2002). A common tool to help us in these efforts is Population Viability Analysis (PVA). With PVAs, information on a species biology, demographics and genetics are combined to understand and simulate trends in populations under different scenarios (Ruggiero et al. 1994, Groom and Pascual 1998, Alçakaya 2005).

Eizirik et al. (2002) developed a PVA for the jaguar population in the Upper and Lower Paraná rivers. They addressed the viability of the jaguar populations within the ‘Green Corridor’ in the borders of Brazil, Argentina, and Paraguay. They performed this analysis based on the information available and used Vortex computer simulations (Lacy 2003) to estimate a minimum viable population and to assess what life-history parameters have the strongest impact on the outcome of the simulations. Their results indicated that quite large population sizes with a carrying capacity of around 650 individuals or active management may be required for long-term persistence of jaguar populations. They also concluded that some biological and ecological parameters appear to have a very strong influence on the outcome of the simulations, particularly those which directly affect reproduction and mortality rates of adult females (Eizirik et al. 2002).

In this chapter I update this first attempt by Eizirik et al. (2002), at a jaguar PVA, by incorporating additional populations, new spatial data, and updated input parameters such as density, home range and habitat selection described in the previous chapters. I used RAMAS/GIS (Akcakaya 2002) software to conduct the

PVA by linking landscape data from geographical information system analysis with a demographic metapopulation model based on input parameters from the available literature and this study. RAMAS/ GIS program (Akcakaya, 2002) has also been used in other studies to combine landscape data with demographic data for helmeted honeyeater (*Lichenostomus melanops cassidix*), California gnatcatcher (*Polioptila californica californica*), and spotted owl (*Strix occidentalis caurina*)(Akcakaya et al. 1995; Akcakaya and Atwood, 1997; Akcakaya and Raphael 1998, Akçakaya et al. 2002, Haines et al. 2006).

The objectives of this study were to: (1) develop a landscape map for the Upper Paraná Region that identifies important areas for jaguar conservation, (2) develop a habitat suitability model for jaguar conservation in this region, (3) link this model to a jaguar metapopulation model for viability analysis of the species, (4) analyze the sensitivity of the viability of this species to different protection scenarios in model parameters, and (5) identify strategic habitat patches and transit stepping stones for dispersing jaguars that could improve the dispersal potential of corridors. Using a habitat suitability map identified by radio collared jaguar, I make recommendations for landscape management and corridor restoration in a human-dominated landscape. It is my hope that these results will contribute to future efforts by state and national government, and well-founded conservation policies in the Upper Paraná ecosystem, that provide the basis for long-term landscape conservation planning within the Upper Paraná Region.

7.2 Study Sites

This study was carried out in the Morro do Diabo in the State of São Paulo and in Ivinhema State Park in the State of Mato Grosso do Sul. Detailed information about these two specific study sites is provided in Chapter 2.

7.3 Methods

7.3.1 Radiotelemetry

Chapter 4 has described the capture, collaring and monitoring of the radio collared jaguars.

7.3.2 The PVA Model

The metapopulation dynamics of the jaguar were modelled in an approximately 5.000 km^2 region of the Upper Paraná-Paranapanema region, extending for 50 km on each side Paraná and Paranapanema Rivers, and from the towns of Teodoro Sampaio (22˚31'36 S; 52 10'09 W) to Santa Terezinha de Itaipu (25˚21'36 S; 54 28'36 W) in Brazil (Figure 7.1). The software RAMAS GIS, was used to develop a habitat suitability model based on land cover and on habitat selection by jaguars. This model was used to calculate the spatial structure of the metapopulation, including size and location of main habitat patches and the distances between them. A combination of my own data and a literature review was used to estimate parameters such as survival, fecundity and dispersal. These parameters were then combined with the spatial structure to build a stage-structured, stochastic, spatially explicit metapopulation model. Finally, this model was used to simulate the dynamics of the jaguar metapopulation and to estimate its viability under various scenarios. The components of the model are detailed below.

7.3.3 Habitat Model

The spatial structure of the jaguar metapopulation in the Upper Paraná-Paranapanema Ecoregion was based on habitat data. This link between habitat data and the metapopulation model was made possible by the Spatial Data program built in RAMAS GIS software (Akçakaya 2005). The program uses spatial data on habitat requirements of the species, such as GIS-generated maps of land cover and combines these data into a map of Habitat Suitability (HS) with a habitat function. This map was then used to find habitat patches by identifying areas of high HS where jaguar population might exist and still survive. The habitat and jaguar location data that formed the basis of this preliminary analysis were from the Morro do Diabo State and the Ivinhema.

Figure 7.1. Jaguar metapopulation dynamics were modelled. Within an area of approximately 50.000 km^2 of the Upper Paraná region, covering the range of 50 km of each side Paraná and Paranapanema Rivers and from the town of Teodoro Sampaio (22˚31'36 S; 52 10'09 W) to the town of Santa Terezinha de Itaipu (25˚21'36 S; 54 28'36 W) in Brazil (Source: Google Earth).

Topographic map layers and habitat categories mainly included those most likely to explain jaguar habitat patches and metapopulation spatial distribution (Table 7.1). These maps were prepared from LandSat Images using both ground knowledge and unsupervised classification of the three Landsat 7ETM satellite images that covered the Morro do Diabo region. The analysis was done with Erdas Imagine 8.4 and Arcview 3.3/Spatial Analyst.

The term *habitat* was used to describe a layer of proportions of a habitat class as defined by vegetation type or other classifying factors used by, or available to, an animal. Each habitat composition summed to 100%. As in Chapter 6, error in assigning an individual radio-location to a particular habitat class assumed that a jaguar used all habitats within a 100 m radius of a radio-location in proportion to the area of that habitat within the circle.

7.3.4 Habitat Selection

Habitat selection was determined as the distribution of all independent jaguar locations in each habitat type in relation to the habitat availability during the study period. Habitat selectivity was then defined by comparing availability (*A*) and utilization (*U*), using Ivlev's (1961) index of selectivity = $(U - A)/(U + A)$. Habitat selection was evaluated at gross scales that provide a broad view of habitat requirements, and whether jaguar use of habitat categories occurred in proportion to their availability in the study site (Table 7.1).

Table 7.1.Habitat availability, use and selection by jaguars in the Upper Paraná.

Habitat type	Symbol	(A) Availability Proportion in the study site (%)	(U) Use: Proportion of jaguar locations (%)	Ivlev's Index of selectivity
Water	water	6.997	4.104	-0.26057
Primary forest	primfor	5.239	13.841	0.45087
Secondary forest	secfor	2.605	5.153	0.32848
Alluvial forest	aluv	0.970	1.025	0.02754
Dense marshland	densemarsh	4.977	10.045	0.33734
Open marshland	openmarsh	11.013	25.695	0.39995
Agriculture	agric	17.208	17.921	0.02030
Pasture	pasture	50.991	22.216	-0.39307

Based on these results, I defined (HS) as:

0.00203*[agric]+0.00275*[aluv]+0.03373*[densemarsh]+0.04000*[openmarsh]-0.03931*[pasture]+0.04509*[primfor]+0.03285*[secfor]-0.02606*[water]

The symbols within brackets refer to map layers (Table 7.1). All map layers were based on the same vegetation map. Each cell of a layer gives the proportion of one habitat type in a grid cell of 300 m by 300 m. This habitat suitability function determines the suitability of a location given various input maps describing environmental variables. In other words, it attempts to identify habitat patches from the jaguars' point of view. This function is used to calculate the habitat suitability for each location (cell) in the map.

7.3.5 Linking the Habitat Map to the Metapopulation Model

The link between the habitat map and the jaguar metapopulation was characterized by two parameters. Firstly, a *threshold habitat suitability HS* was set as the minimum habitat suitability value below which the habitat is not suitable for reproduction and/or survival. Based on field evidence of other jaguar locations along the entire Upper Parana basin, a value of 1.2 was used as the threshold HS. The proportion of the study area with threshold habitat suitability at or above 1.2 is 9.1%. Thus, this represents a conservative or a precautionary value, because only a small portion of the landscape was assumed to be suitable. Secondly, *neighbourhood distance* was used to identify nearby grid cells that belong to the same patch (i.e., subpopulation) and may represent the mean foraging distance of the species or the size of the home range. Based on the average home range area of 115.9 km^2 ± 42.6 km^2, the diameter of a circle shaped home range was calculated as 40 to 53 cells (1 cell=300 m). The more conservative value of 40 cells or 12 km was used.

Based on the habitat map (see above), and these two parameters, RAMAS GIS (Akçakaya 2005) identified the patch structure, which includes the size and location of habitat patches. Each patch supports one subpopulation of the metapopulation. This method of patch identification is described in Akçakaya et al. (1995) and Akçakaya (2000). This analysis resulted in 3 populations (see Results below), in which population 1 was the Morro do Diabo population.

7.3.6 Density Dependence and Initial Abundance

After the populations (habitat patches) were identified, the carrying capacity (K) and initial number of individuals was calculated for each patch, using the total habitat value of each patch. Based on home range sizes and the camera trapping results, the carrying capacity was estimated for the Morro do Diabo population as 18 animals (including only adults and sub-adults of both sexes). The carrying capacity was then scaled to the other populations based on the total HS of the Morro do Diabo population, which was 15617. Thus, the carrying capacities of the other populations were calculated by multiplying their total HS value by 0.001153 (18/15617). A ceiling-type density dependence model was assumed where the population grows exponentially until reaching a ceiling population size (i.e. carrying capacity) and remains at that level (Akçakaya 2002) for each jaguar population. The carrying capacities were calculated based on habitat data as population ceilings. This type of density dependence may occur with jaguars when all territories are occupied. Initial abundance was assumed to be equal to carrying capacity for all populations, and distributed by age classes according to a stable age distribution.

7.3.7 Demographic Structure and Vital Rates

A stochastic, age- and sex-structured model was developed with annual age classes. Some demographic parameters of the model were based on the model developed by Eizirik et al. (2002), who used parameters inferred from available field and captive data on jaguars and related species (Sadleir 1966, Schaller 1972, Ewer 1973, Schaller and Crawshaw 1980, Miller and Everett 1986, Rabinowitz and Nottingham 1986, Martin and de Meulenaer 1988, Oftedal and Gittleman 1989, Seymour 1989, Crawshaw and Quigley 1991, Smith and McDougal 1991, Bailey 1993, Beier 1993, Oliveira 1994, Crawshaw 1995, Nowell and Jackson 1996).

My field observations of the higher density of the Morro do Diabo population were incorporated by assigning higher fecundity to this population. Rather than the litter size of 2.75 (Eizirik et al. 2002), a litter size of 3.0 was assigned for the Morro do

Diabo population, and a lower litter size of 2.5 was assigned for the other populations. The age of first reproduction was specified as 2 years, with an average birth interval of 2 years, and a sex ratio of 50% females. Thus, maternity (m) of an adult female was calculated as 0.625 (low) to 0.750 (high) daughters per female. Maternity of 2-year old females (m_2) was half of that of 3-year old and older females. The matrix model used parameters according to pre-reproductive census. Thus, fecundity was calculated as $F=m \cdot S_0$, where S_0 is survival rate from birth to age 1. The same survival rates were assumed as used by Eizirik et al. (2002), except for composite age classes of females older than 4 and males older than 5 years of age that were assumed to have survival rates of 50% of the survival rate of the preceding age class (Table 6.2).

Table 7.2. The "high" stage matrix used in the model for the Morro do Diabo population. "Fem" and "Male" indicate female and male age classes, respectively. The matrix is parameterized according to pre-reproductive census. Thus, the first age classes (Fem 1 and Male 1) include individuals that are almost 12 months old. For the other populations, the fecundities (rows marked Fem 1 and Male 1) were 17% lower based on a litter size of 2.5 instead of 3.0.

	Fem 1	**Fem 2**	**Fem 3**	**Fem 4**	**Fem 5+**	**Male 1**	**Male 2**	**Male 3**	**Male 4**	**Male 5**	**Male 6+**
Fem 1	0	0.2475	0.495	0.495	0.495	0	0	0	0	0	0
Fem 2	0.83	0	0	0	0	0	0	0	0	0	0
Fem 3	0	0.81	0	0	0	0	0	0	0	0	0
Fem 4	0	0	0.80	0	0	0	0	0	0	0	0
Fem 5+	0	0	0	0.80	0.40	0	0	0	0	0	0
Male 1	0	0.2475	0.495	0.495	0.495	0	0	0	0	0	0
Male 2	0	0	0	0	0	0.83	0	0	0	0	0
Male 3	0	0	0	0	0	0	0.65	0	0	0	0
Male 4	0	0	0	0	0	0	0	0.70	0	0	0
Male 5	0	0	0	0	0	0	0	0	0.70	0	0
Male 6+	0	0	0	0	0	0	0	0	0	0.70	0.35

7.3.8 Dispersal Rates

Dispersal between populations was modelled using a dispersal distance function, based on centre-to-edge distances between populations. Distances were measured from the centre of the source population to the edge of the target population. Centre-to-edge distances are used to model asymmetric rates of dispersal expected between two habitat patches that are substantially different in size (Akçakaya and Raphael 1998). This resulted in a dispersal matrix with 0.0 to 3.3% dispersal rate among populations (Table 7.3). Density dependence was modelled into dispersal for each population, and the dispersal rate was directly proportional to population size. Under density-dependent dispersal, when the population size (*N*) is lower than the carrying capacity (K), the proportion dispersing is lower in proportion to the ratio of *N*/*K* (Akçakaya and Atwood 1997). In addition, stochasticity was modelled into dispersal by sampling dispersal rates from a normal distribution with a coefficient of variation of 20%.

Table 7.3. Dispersal matrix used in the model, showing the proportion of individuals moving from each population (columns) to other populations (rows). Thus, 3.29% of individuals move from population 1 in Morro do Diabo to population 2.

	Pop1	**Pop2**	**Pop3**
Pop1	-	0.63%	0
Pop2	3.29%	-	2.47%
Pop3	0	0.77%	-

7.3.9 Stochasticity

Environmental stochasticity was modelled by sampling mortality, fecundity and dispersal rates from random distributions with coefficients of variation of 20%. This value was similar to the variability of mortality included in the model of Eizirik et al. (2002). An important source of environmental fluctuations was frequent fires, which are more common in hotter and drier years. Because such patterns would affect all sub-populations simultaneously, environmental fluctuations would be expected to be correlated to some extent. However, the correlation would not be perfect, because there are other, more local, sources of environmental variability, such as hunting and other human disturbances. Thus, environmental fluctuations were assumed to be moderately correlated among populations, based on a correlation-distance function that resulted in correlation coefficients ranging from

0.04 to 0.22. Demographic stochasticity was also used in the number of survivors, number of offspring and number of dispersers (Akçakaya 1991).

7.3.10 Simulations and Scenarios

A series of simulations was used to analyse the dynamics of the jaguar population using the model described above. Each simulation consisted of 1,000 replications and each replication projected the abundance of each population for 50 years, which corresponds to 20-25 generations. The model described above assumes that current conditions of habitat and demography will remain unchanged in the future. To compare this scenario to what might be expected under protection, a "protection scenario" was developed with the following assumptions. Under protection, the carrying capacity of populations 2 and 3 would increase gradually to reach double their current carrying capacities, and then remain at this higher level. In practical terms, this “protection scenario” could be achieved by fire prevention measures, avoiding poaching and jaguar-human conflicts, protect prey populations, and enforcing rules and regulations in populations 2 and 3 identified by this study. Under protection the average fecundity of these two populations would be assumed to reach that of population 1 in Morro do Diabo in 10 years. All parameters of population 1 including the carrying capacity and average fecundity were assumed to remain at their current values.

7.4 Results

7.4.1 Patch Structure

The habitat model produced the habitat map (Figure 7.2) and a patch structure with 3 patches of suitable cells within the neighbourhood distance of each other (Figure 7.3). These patches covered a total area of 4.105 km^2 and had a total carrying capacity of 126 individuals (Table 7.4). The patch structure was realistic considering the remaining habitat, known jaguar occurrences and the location of some protected areas in the Upper Paraná-Paranapanema region.

The largest patch for population 2 had an area of 2.224 Km^2 and comprised the Ivinhema region and a large area to the south towards the Ilha Grande National Park, where considerable jaguar populations are known to occur. This patch made up about 54% of the total area of all patches combined and had a carrying capacity of 64 individuals. The three suitable patches covered only 3.39 % of the total landscape analyzed, a very small area considering the area requirements of jaguar. Patches have gaps between them, which represent unsuitable locations relative to the jaguar’s habitat requirements and foraging distance. Major gaps occur between the Morro do Diabo Region (population 1) and the Ivinhema State Park (population 2) and again, between Ivinhema and the southern populations identified in Eastern Paraguay along the Paraná River (Patch 3). However, no gaps were identified between the Ivinhema and the Ilha Grande National Park. The landscape between these two protected areas appeared suitable for jaguars to establish their home ranges and dispersal when the species habitat requirements and foraging distance were considered. Landscape gaps identified between the 3 sub-populations might affect landscape connectivity and dispersal between them. The habitat suitability map has great potential to be used to identify stepping-stone corridors. These are cells with high suitability value outside the patches identified and can link jaguar subpopulations. They can also contribute to the design and restoration of a interconnected landscape.

Figure 7.2. Habitat Suitability Map in the Upper Paraná region. Values for habitat suitability are represented in the scale below, with HS values ranging from – 3.9 (in red and least suitable) to + 4.5 (in green and most suitable).

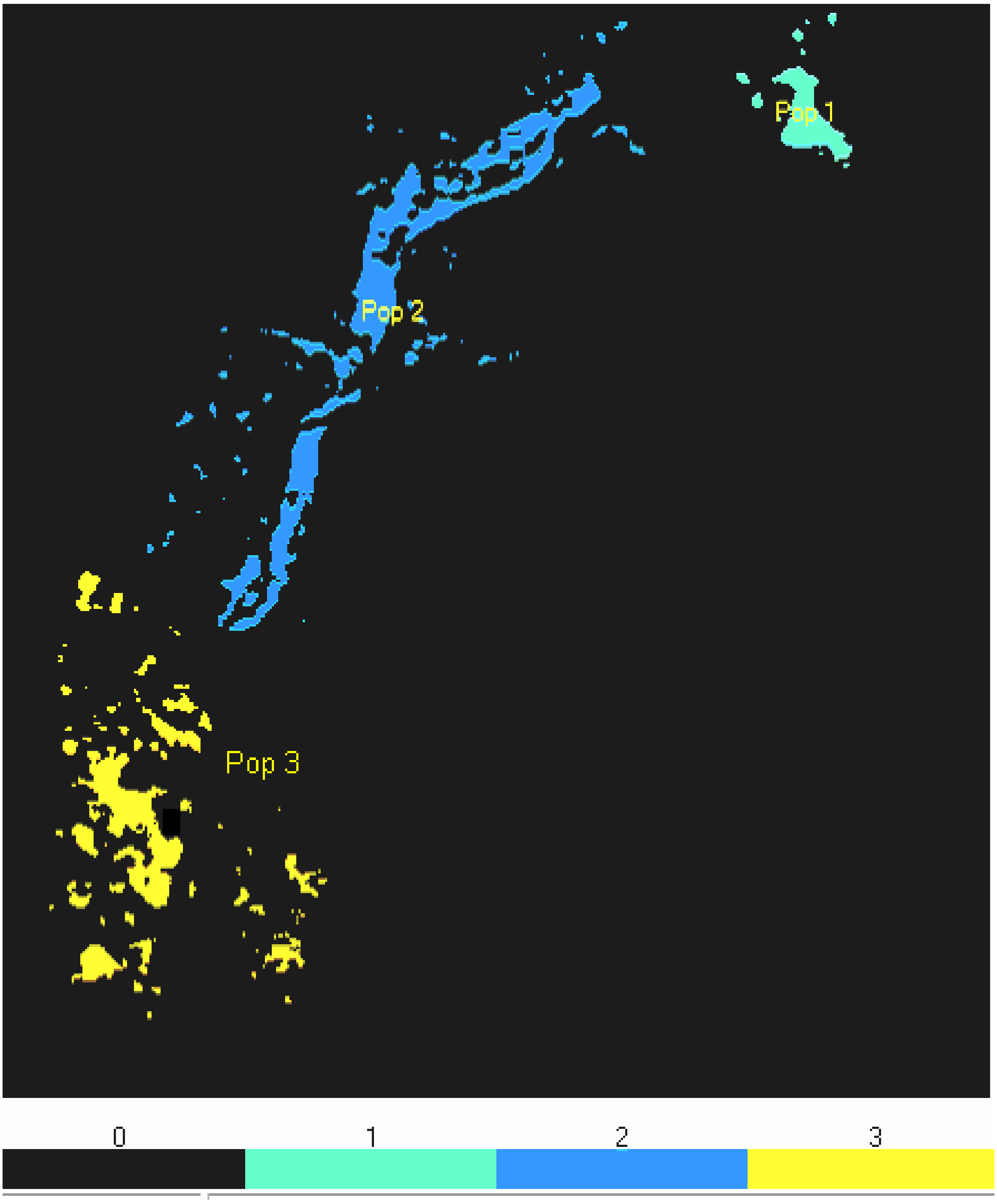


Figure 7.3. Patch structure of jaguar sub populations identified by the model in the Upper Paraná region

Each colour indicates one habitat patch identified by the programme. Patch 1 corresponds to the Morro do Diabo region in São Paulo State (Brazil). Patch 2 corresponds to the Ivinhema region in Mato Grosso do Sul State and Ilha Grande National Park region in Paraná State, both in Brazil. Patch 3 corresponds to jaguar sub-populations in eastern Paraguay along the Paraná River, and more specifically to the states of Canindeyú (Salto de Guairá) and Alto Paraná (Ciudade del Este), comprising an area with a series of protected areas such as Refugio Biológico Carapá, Reserva Natural Privada Itabo, Reserva Natural Privada Morombi, Reserva Biológica Mbaracayú, Reserva Biológica Pikyry, Refugio Biológico Tati Yupi, Reserva Biológica Itabo and Reserva Biológica Limoy.

Table 7.4. Results of patch identification. Total Habitat Suitability (HS) is the total value of the habitat suitability values (as described above and given in Figure 7.3) in all cells included in a patch.

Patch #	Population Name*	Total HS	Area (km²)	Area as Patches %	% Landscape	Carrying capacity (K)
1	Morro do Diabo State Park Region (São Paulo State)	15617	409	9.97	0.84	18
2	Ivinhema State Park Region (Mato Grosso do Sul State) and Ilha Grande National Park Region(Paraná State)	55422	2224	54.57	1.34	64
3	Eastern Paraguay along the Paraná River, and more specifically to the states of Canindeyú (Salto del Guairá) and Alto Paraná (Ciudad del Este), comprising an area with a series of protected areas such as Refugio Biológico Carapá, Reserva Natural Privada Itabo, Reserva Natural Privada Morombi, Reserva Biológica Mbaracayú, Reserva Biológica Pikyry, Refugio Biológico Tati Yupi, Reserva Biológica Itabo and Reserva Biológica Limoy	38404	1472	35.86	1.22	44
	Total:	109443	4105	100%	3.39%	126

* Including areas in the mosaic surrounding the current protected areas.

7.4.2 Population Viability

Under the "current" scenario, the metapopulation tended to decrease (Figure 7.4). The median time for decline to half of the initial abundance (i.e., from a carrying capacity of126 to 63) was about 18 years, and the risk of extinction within the next 50 years was predicted at about 25%. Expected minimum metapopulation size, which is the minimum metapopulation size during the 50-year projection interval, averaged over the 1,000 replications was about 17 individuals. At the end of the 50 years, the average predicted metapopulation size was about 21 individuals (Figure 7.4), median metapopulation size was 14 individuals, and average number of extant populations or occupied patches was 1.4 (Table 6.5).

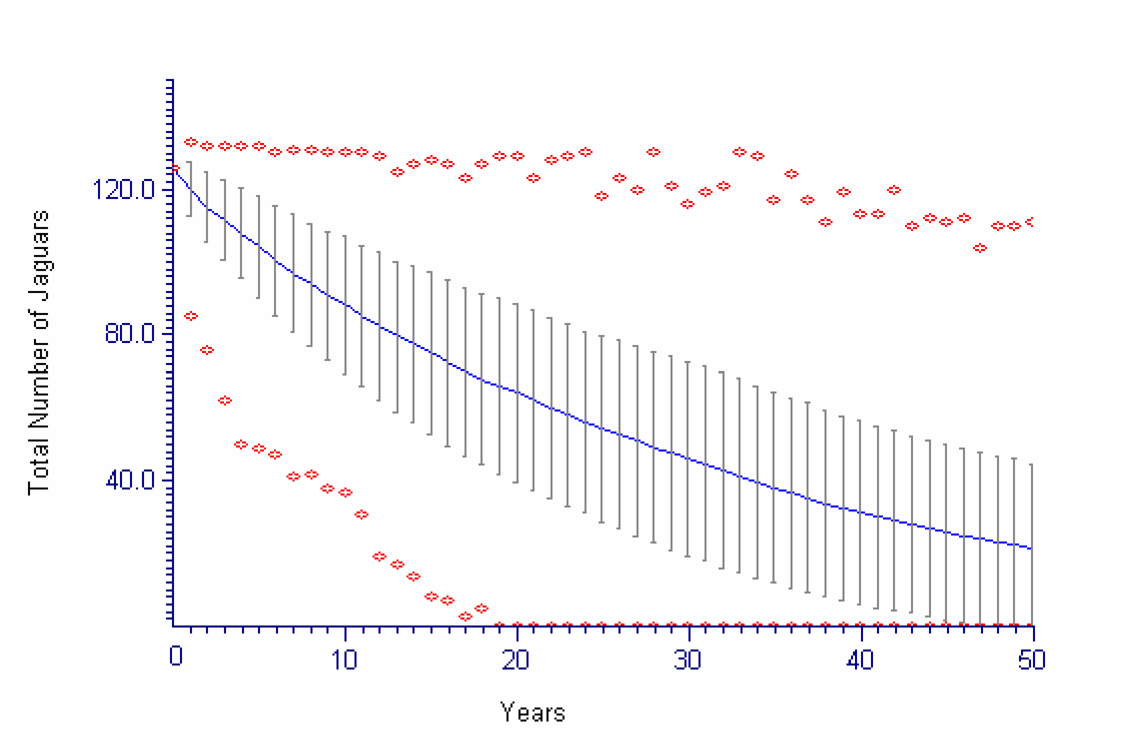


Figure 7.4. Predicted metapopulation size comprising total number of jaguars in the 3 sub-populations, in the next 50 years under current conditions. The blue line represents the average of 10,000 replications, error bars indicate plus and minus 1 standard deviation, and red markers indicate minimum and maximum population sizes over the 10,000 replications for each year.

Table 7.5. Viability results under the "current" and "protection" scenarios.

Viability result	**Scenario**	
	"Current"	***"Protection"***
Median time to decline to half of initial size	18 years	>100 years
Risk of extinction within the next 50 years	25%	1%
Expected minimum metapopulation size	17	84
Final average metapopulation size	21	165
Final median metapopulation size	14	180
Final mean number of extant populations	1.4	2.7

The results under the "protection" scenario were quite different (Table 6.5). Under this scenario, the metapopulation was stable with a low risk of extinction, a high predicted abundance, and a high occupancy. There was substantial and statistically significant differences between the two scenarios in terms of risks of extinction and decline (Figure 7.5). The probability of a 58% decline from 126 to 53 was about 0.1 under "protection" scenario (lower curve) and about 0.9 under the "current" scenario, with a difference of about 0.8 between the two scenarios.

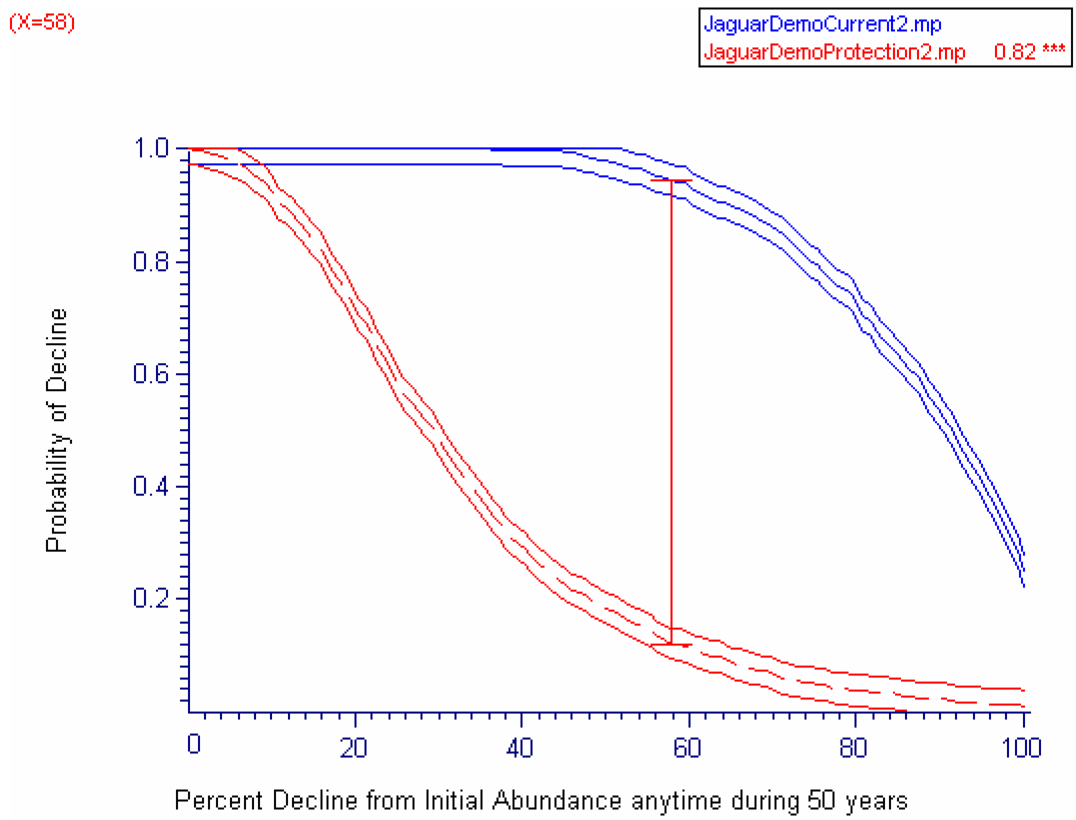


Figure 7.5. Probability of decline for different amounts of decline (as percentage of initial population size). The right end of the curves (100%) corresponds to extinction. The vertical bar shows the largest difference between the curves (at x=58%).

7.5 Discussion

The threats, ecology and distribution, and management options of the jaguars in the Upper Paraná River Corridor necessitate the use of models to evaluate options for their conservation and management. The results of spatial distribution of jaguars in this region, and their dispersal ecology and demography suggested a metapopulation structure, with distinct but interacting local sub-populations inhabiting relatively suitable habitat patches separated by less suitable areas. The jaguars in this region are threatened by several factors, including habitat loss, habitat fragmentation, road mortality, and mortality resulting from their interaction with livestock (Crawshaw et al. 2004, Cullen et al. 2005, Lansdorf et al. 2006). Each of these factors affects a different aspect of the jaguar metapopulation. There are also several possible types of management actions that may benefit these populations, including habitat protection, increasing connectivity, decreasing road mortality, habitat enhancement or restoration (Eizirik et al. 2002, Cullen et al. 2005). To evaluate the effectiveness of such a diverse set of management options requires a method that can integrate diverse types of information into a single assessment framework. It also needs to incorporate a variety of factors and the interactions for a population under a variety of threats, and a fragmented distribution in the landscape. One of the most important strengths of the landscape detective model is the integration of information and in particular the integration of the metapopulation models.

Previous population viability analyses (PVA) for jaguars in the Upper Paraná River have combined information on biology, demographics and genetics to understand and simulate trends in populations under different scenarios. Eizirick et al. (2002) concluded that the parameters that had the strongest impact on population viability were those directly related to birth and death rates of jaguars. In their analysis, mortality rates, especially among females, were key to population persistence. Management strategies which imply increased mortality of adult females should be avoided. Similar observations have been made in PVAs performed for other large cats (Martin and de Meulenaer 1988, Berry 1996, Karanth and Stith 1999, Haines et al. 2006). However, some of these studies are not comparable to this study in terms of specific focus or analytical approach. This comparison does indicate population characteristics which may be common to the genus *Panthera* or to felids in general.

The importance of increasing vital rates for jaguar subpopulations was also shown by Cullen et al. (2005) in a preliminary PVA simulation. The preliminary analysis also predicted declines and risk of extinction of the jaguar population in the Upper Paraná. The negative effect of natural dispersal was noteworthy. When dispersal was modelled in the identified patches, the model outputs were very similar in terms of population viability. This was explained by the source and sink dynamics of small and unstable populations. However, sensitivity analysis showed significant results when dispersal was combined with a 15% increase in the populations vital rates by increasing survivorships and decreasing mortality rates (Table 7.6). A similar result was obtained by including the jaguar population of the Iguaçu National Park in the model. The metapopulation and all identified populations were likely to persist and stabilize when this scenario was used. In the short term, increasing vital rates through greater fecundity and decreased mortality seems more important than increasing dispersal rates. Increasing dispersal, specifically for the Upper Paraná metapopulation is only recommended once a more stable jaguar populations is reached.

Table 7.6. Sensitivity of results to different parameters and scenarios used when modelling the viability of the Upper Paraná-Paranapanema jaguar metapopulation.

Parameter/Scenario	Effect	Terminal [a] extinction risk	Metapop [b] occup.	MDO	IVO	IGO
Base model	-	65%	12	2	8	2
Base model + 10% dispersal rate	-	100%	5	1	3	1
Base model + 10 disp.rate + 15% vital rates	+	1%	42	12	20	10
Base model + 10% nat. dispersal + Iguaçu Park	+	0%	65	3	3	6
Base model + 10% nat.disp + transloc + Iguaçu	+	0%	74	10	11	6

a. Shows the probability that the metapopulation abundance will end up below a threshold number of 10 individuals 50 years from now;

b. Metapopulation occupancy: shows the total number of individuals the metapopulation is likely to have 50 years from now;

MDO= Morro do Diabo Area occupancy in 50 years;

IVO= Ivinhema Area occupancy in 50 years;

IGO= Ilha Grande Area occupancy in 50 years.

Transloc= translocations or managed dispesal at 10 % rate among all populations.

Another aim if this analysis was to demonstrate the viability of adding another population to the Upper Paraná-Paranapanema jaguar metapopulation. This was done by including in the simulations the southern most protected jaguar population in Brazil – the Iguaçú Falls State Park. For Iguaçú, the values used for population carrying capacity was (K=40) and initial abundances of 67 individuals (Crawshaw et al. 2003). Considering this scenario, it is also very important to emphasize that jaguar natural dispersal between Iguaçu and the Upper Paraná-Paranapanema region is possible, when one considers dispersal distances of the species and the major forest restoration programmes going along this corridor. I also justify the need of major community based conservation programmes such as the ones described in Chapter 3. Model results showed positive effects, mostly if we also include translocation in a management program in combination with natural dispersal where it is realistic possible (Table 7.6). Natural dispersal will be greatly enhanced with forest plantations along the corridors identified by the landscape detective model.

A recent risk assessment of jaguar populations in Missiones, Argentina also emphasized that jaguar population dynamics are sensitive to adult survivorship, and even minor decreases in adult survivorship leads to population declines (Erick Lansdorf, pers comm). Lansdorf concludes that reducing the effects of road kills or any other source of adult mortality will improve the long-term viability of the population. The results of the model strongly indicate that increasing habitat will only benefit the jaguar if the other threats to which jaguars are exposed such as roads and poachers are minimal.

These findings point to the importance of increasing vital rates for jaguar subpopulations. According to my landscape detective model, the estimated jaguar metapopulation of 126 individuals in the 50.000 km^2 region of the Upper Paraná region is not viable in the long term. Although this result is based on best information currently available, it is important to note that it is also likely to incorporate some degree of uncertainty. Ongoing work and analyses will allow us to quantify this uncertainty.

The "protection" scenario is based on the assumption that all areas identified as good habitat patches will be well managed by the local authorities and park administrators. In practical terms, this protection scenario could be achieved by fire prevention measures, avoiding poaching and jaguar-human conflicts, protect prey populations, and enforcement of rules and regulations in good habitat patches identified by the model. These measures are very likely to decrease jaguar mortality and have important consequences for fecundity rates and cub survival. The difference between the two scenarios is substantial, and demonstrates the potential effect of conservation action on the persistence of this species in this landscape. However, it is important to note two limitations. Firstly, the protection scenario is not spatially explicit. A set of spatially explicit scenarios would involve protection of different combinations of parcels of available and suitable land, in relation to currently existing protected areas (Akçakaya et al. 2007). In the absence of a detailed survey of land ownership and availability, I used a simpler approach of simulating the expected overall effects of protection in terms of improved habitat and vital rates. As a result, I simulated only a single protection scenario, whereas a spatially explicit set of options would allow simulating multiple scenarios that may involve similar amounts of land protected, but with different spatial configurations. Secondly, the uncertainties mentioned above must be incorporated when comparing multiple scenarios.

The sensitivity of this analysis suggests that these preliminary results should not be interpreted in absolute terms. It would be inappropriate to use these results to conclude that the jaguar metapopulation in the Upper Paraná basin is in threat of extinction. There is simply too much uncertainty about most of the parameters to predict with confidence what the population size will be in 50 years or what is the risk of extinction. Despite this uncertainty, these models can have practical use in two ways (Alçakaya and Atwood 1997). First, they give information about which parameters need to be estimated more carefully and where funds and field work effort should concentrate. Second, they allow us to rank management options in terms of their predicted effect on the viability of the target species. As this work progresses and more demographic and ecological data accumulate, it will be possible to come up with more realistic results and pragmatic management recommendations

CHAPTER 8

CONCLUSIONS

In this thesis I use the jaguar (*Panthera onca*) as a landscape detective. A landscape detective is defined as an organism that can help obtain information and evidence from landscapes on how to design and manage protected area networks, because their requirements for survival show us factors important to maintaining large core and connected landscape in ecologically healthy conditions"

Specifically, this top carnivore species is used to detect and develop a network of core reserves for the Upper Paraná Region in Brazil. In this region, the remaining forest fragments combined with its marshlands still harbours the last remaining jaguar populations in the Atlantic Forest. These are critical areas for jaguar conservation and considered among the few areas where large carnivores such as jaguars, pumas and ocelots might persist in the long-term, if well managed. The landscape in the Upper Paraná Region offers a good scenario to apply the landscape detective approach, because the ongoing destruction of forests and marshlands are confining the remaining jaguar populations into networks of small patches of suitable habitat. A spatial metapopulation conservation model was developed using the jaguars as the landscape detective includes the first-order effects of patch area and isolation on extinction and colonization.

The landscape detective approach for jaguars is comparable to similar focal species approaches for site-based conservation. However, the landscape detective approach is different in that it is more species-intrinsic, because the jaguar specific habitat requirements are the central point. Using VHF and GPS telemetry, the jaguar habitat requirements provided by habitat selection analysis was used to build a habitat suitability function to define the landscape in which conservation must be done. This approach is not only a model, but a practical tool to develop species landscape conservation actions.

Two assumptions lie behind the use of large carnivores as conservation tools. The first relates to *efficiency*, in that the area required for the persistence of jaguar populations is larger than that required by most other species in the region. The jaguar range should be large enough to encompass the habitats of other sympatric species, hence large-carnivore conservation will ensure the protection of the rest of biodiversity sharing the same range. The second assumption is *functional*, in that the jaguar plays a critical role in the system. The disappearance or removal of the jaguar would result in a degraded and simplified ecosystem (top-down effects).

The landscape detective model must be realistic and supported by good data to give reliable results that can be used in conservation and management. This is only possible if relevant data are available, and are analyzed to provide unbiased estimates of the model parameters. For modelling the jaguar metapopulation in the Upper Paraná River Corridor, and evaluating the available management options, one of the most important factors to consider is spatial structure, which is simply the characteristics and spatial arrangement of the habitat suitable for jaguars.

The data required for developing the landscape detective tool include information on habitat preferences, use and availability, and the relationship between habitat and demography. The data that are often used to provide this information include habitat selection, population density estimates, home range size, presence/absence and other measures of demography in different habitat types. In addition, data on vital rates including survival, fecundity, and dispersal, their temporal variability, and their relation to population abundance are used in habitat-based models. Hence, the core data chapters of this dissertation aim to provide these data to develop the landscape detective tool.

In this thesis, chapter 3 presents an analysis of local land reform and how this impacts conservation in the Atlantic forests. A comparison is made with similar experiences in different areas. Where land reform groups are better organized, technical cooperation on settlement agriculture permitted the exploration of mutual interests in conciliating the productive landscape with conservation of species such as the jaguar. The landscape detective tool can be used to help set priorities in the implementation of these landscape conservation actions.

Chapter 4 provides information on jaguar density in the Morro do Diabo State Park, one of the two study sites used for field work. Chapter 4 not only provides density date, but also verifies the density estimates derived from two methods, using both camera trapping (capture-recapture models), and VHF and GPS telemetry. Camera trapping generated a density of 2.47 jaguars per 100 km^2. With radio telemetry, the overall density of jaguars was 2.20 jaguars per 100 Km^2 and based on confidence interval inference, there was no statistical difference between both estimates. Caution should be taken by other researches when using the Mean Maximum Distanced Moved (MMDM) derived from camera trapping to report density estimates. Results from the analysis suggest that camera trapping methodology should be used in conjunction with other monitoring techniques to better reflect the true ranges of animals to estimate the effective sample area, and adjust density estimates accordingly. The small jaguar population size estimated for Morro do Diabo State Park, around 15-18 individuals, is not viable in the long term. However, when density estimates are extrapolated for the whole Paraná Basin, a viable jaguar metapopulation may persist.

Chapter 5 evaluated jaguar home ranges and movements for 10 individuals in Morro do Diabo State Park and Ivinhema State Park (ISP). When data from both sexes and study areas are combined in the analysis, dry season home ranges were similar to wet season home ranges. The mean annual and multiyear 85% home ranges were larger than those reported by previous studies. Some individual core areas overlapped intensively and the presence of cattle may have attracted habituated individuals to these “easy prey” areas, explaining their smaller home ranges and smaller distances moved. The mean yearly distances moved between consecutive locations for all 10 individuals studied averaged 2.76 km and the maximum distance moved by all jaguars between consecutive locations averaged 13.18 km. Occasional movements of male jaguar were 30 km long and required these male jaguars to traverse open pastures and gallery forests in very short periods of time. Based on this information, it appears that jaguars are good candidates for landscape detective species in this region and for designing conservation landscapes that capture other important elements of biodiversity. For example, during their movements within their home range and during dispersal, jaguars can help to identify strategic transit refuges or stepping stones that could improve the dispersal potential of corridors between the identified suitable habitat patches.

Chapter 6 assessed habitat selection by jaguars at second and third-orders of selection. The results show that jaguars consistently preferred primary forests and dense marshes and avoided human-dominated areas such as intensively managed open pastures. Two major conclusions are drawn from these results.

First, dense marshes along riparian vegetation ranked first in use for most jaguars. Dense marshes are the only potential jaguar habitat remaining that continuously connects the remaining suitable patches and protected areas along the Paraná River basin. Hence, these productive marshlands may facilitate natural dispersal and allow genetic exchange among jaguar subpopulations. The habitat selection analysis supported the notion that jaguars are a good candidate for a landscape detective species in this region, since marshlands were highly selected by most jaguars and dispersal and connectivity are needed for the metapopulation conservation.

Second, when third order habitat selection was analyzed, it was found that jaguars moved their core areas from marshlands to upland and pastures. Some individuals became established in areas of intensive private cattle ranching and calving and could come into conflict with farmers because of predation on livestock. If jaguar dispersal is hampered, because poaching by farmers, this could negatively affect the source-sink dynamics of subpopulations and destabilize the metapopulation in the long term. Jaguars have the ability to live and disperse in marshland habitats. However, their movements could be frustrated by cattle ranching environments. Key private properties can be identified by the jaguars and these are should be protected.

Chapter 7 used information from the previous chapters to construct the landscape detective tool to identify and help develop a network of wild core reserves interconnected by viable corridors in the Upper Paraná River. The model resulted in 3 suitable patches with a total area of over 4,000 km^2 and a total carrying capacity of 126 individuals in the Upper Paraná Atlantic Forest. The habitat-based landscape detective model was linked to a population viability analysis which showed that under the current scenario the median time to decline to half of initial abundance (i.e., from 126 to 63) was about 18 years, and the risk of extinction within the next 50 years was predicted as about 25%. However, under a predicted "protection" scenario the metapopulation has a low risk of extinction, a high predicted abundance and a high occupancy. Increasing the vital rate of survivorship and decreasing mortality in the short term has better effects on population persistence when compared to other simulation scenarios, such as increasing dispersal.

8.1 Landscape Conservation Planning

When planning a network of core reserves interconnected by viable corridors in the Upper Paraná River, information on dispersal routes and pathways for jaguars is fundamental. Consequently, the ecological viability of the network connecting core protected areas should be considered dependent on the movement of the species between habitat patches. Information on jaguar dispersal in these highly fragmented landscapes is non-existent. Continued monitoring of the jaguar populations in the study area will provide this information. In this highly fragmented landscape, young jaguar males cannot escape the boundaries of local populations and may be forced to disperse to nearby populations. The small suitable habitat patches identified by the model may function as “stepping stones” and facilitate numerical and genetic flow to more distant protected reserves. Therefore, I hypothesize that by continuing to track dispersing young males I can identify and map stepping-stone corridors linking jaguar subpopulations and contribute to the design of an interconnected landscape. For this, I will continue the efforts in camera trapping and GPS radio tracking in key sites of the Paraná Corridor, more specifically in possible dispersal gaps identified by the spatial analysis of the Paraná Eco-Region.

In the Upper Paraná Region, the time is critical for protecting land areas under a plan that will ensure habitat contiguity with future land development. The jaguar in the Upper Paraná ecosystem represents an endangered population and isolated from the Pantanal and the Coastal Atlantic forests. The distribution of jaguars reflects relative habitat conditions along a human-impacted landscape of importance to wildlife conservation. This study identified three large suitable patches for jaguar conservation, which together were about 4.100 km^2 in area or equivalent to 8% of the potential habitat in the study area. These large patches represent core areas for jaguars in the Upper Paraná Region. They should constitute a proposed region for protected-area management, which may include a combination of different land uses such as intensive use areas, buffer zones or intermediate use areas and some strictly protected areas that could be linked by wildlife corridors and other suitable areas identified by this model. The suitability map also helped in identifying landscape gaps or strategic transit refuges or stepping stones for dispersing jaguars that could improve the dispersal potential of corridors. This information will lead to recommendations for corridor restoration in a human-dominated landscape for jaguar conservation.

8.2 New Protected Areas

The habitat suitability maps developed in this thesis will help to identify new areas for Jaguar conservation and to establish Jaguar Conservation Private Reserves along the study area, involving private landowners adjacent to the already existing protected areas. With these maps the following steps will be taken: 1) conduct field work in identifying and mapping large private properties (> 500 ha) along this specified jaguar range, 2) overlay the limits of all private properties identified, with the Jaguar Habitat Suitability Map and approach potential landowners, 3) select at least 5 potential properties within high habitat suitability areas based on the increase in overall jaguar viability when these areas are assumed to be protected, and 4) in consultation with the owners of selected properties, start the process of applying for a Jaguar RPPN's (Reservas Particulares de Patrimônio Natural - Private Natural Heritage Reserve).

In Brazil, nearly 600 individuals, corporations and activist groups have voluntarily registered private property under the RPPN scheme since 1990. Under the RPPN program, land-use is restricted to research, environmental education and ecotourism. Not all RPPNs are open to visitation by outsiders, but many landowners see ecotourism as a way to ensure both revenue and preservation. These selected landowners will be encouraged in applying for RPPN status with the Brazilian Environmental Institute (IBAMA). When approval is granted, owners receive modest breaks on property taxes and, in principle priority for certain kinds of public financing like cash distributed by the National Environmental Fund (FNMA), a programme backed by the Interamerican Development Bank.

With the continuation of this work I hope some of the landowners identified by my model will join the RPPN conservation approach. The private reserves are a key element in Brazil's "corridor" strategy", a programme considered to be effective in preserving biodiversity. Under the approach, larger areas like national parks and wilderness areas will be linked by corridors to smaller nature reserves that allow species such as the jaguar to roam over a wider area, thus encouraging greater genetic diversity among sometimes dwindling populations.

Ultimately, the fate of the jaguar in the Upper Paraná River, for that matter, of any large predators constrained within relatively small, isolated parks and reserves remain in the hands of the people that live around these areas and coexist with these species. However, it is the responsibility of managing agencies to resolve local conflicts that are inevitable in the interface between the natural and the man-modified worlds. Only through the integration of applied research, implementation of management recommendations derived from these findings, involvement of NGO and Universities, co-management of protected areas, participation of local communities through community-based landscape restoration program, agroforestry extension and environmental education program, and appropriate policies will these species have a chance to survive.

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Appendix 1. Tables with results of jaguar habitat selection

1.1 Across both wet and dry seasons, individual jaguars varied in selection for vegetation types within the study area (second-order selection), but most animals preferred forests and dense marshes than human-dominated landscapes. Each cell gives the percent of area within 100 m radius of radio-locations for each individual within the Morro do Diabo study area (MDSA).

Animal ID	Water	Prim. Forest	Sec. Forest	Alluvial Forest	Dense Marsh	Open Marsh	Agriculture	Pasture
F1	7.36	8.67	10.30	0.50	4.86	14.94	48.35	5.02
F2	0.00	78.49	18.33	0.00	0.00	0.00	3.18	0.00
F3	0.00	88.07	5.73	0.00	3.19	0.02	2.99	0.00
F4	2.66	10.28	4.83	0.16	8.08	36.24	19.22	18.54
F5	0.00	83.33	5.56	0.00	0.00	11.11	0.00	0.00
Female Mean	2.00	53.76	8.94	0.13	3.22	12.46	14.74	4.71
M1	11.02	8.05	4.10	0.03	9.61	17.13	37.13	12.93
M2	11.98	47.93	14.42	0.15	14.15	3.86	6.91	0.60
Male Mean	11.50	27.99	9.26	0.09	11.88	10.49	22.02	6.77
MDSA	**5.33**	**14.88**	**5.66**	**0.05**	**1.25**	**6.02**	**16.58**	**50.20**

1.2 During the dry season, individual jaguars varied in selection for vegetation types within the study area (second-order selection), but most animals preferred forests and dense marshes human-dominated landscapes. Each cell gives the percent of area within 100 m radius of radio-locations for each individual within the Morro do Diabo study area (MDSA).

Animal ID	Water	Prim. Forest	Sec. Forest	Alluvial Forest	Dense Marsh	Open Marsh	Agriculture	Pasture
F1	8.19	10.26	12.46	0.72	3.92	10.40	50.73	3.31
F2	0.00	78.49	18.33	0.00	0.00	0.00	3.18	0.00
F3	0.00	83.75	6.88	0.00	4.79	0.03	4.56	0.00
F4	2.19	13.95	0.35	0.24	8.02	36.19	18.79	20.26
F5	0.00	83.33	5.56	0.00	0.00	11.11	0.00	0.00
Female Mean	2.076	53.956	8.716	0.192	3.346	11.546	15.452	4.714
M1	10.86	9.72	4.96	0.06	12.29	12.79	35.62	13.71
M2	11.77	48.02	15.34	0.16	12.90	3.86	7.29	0.66
Male Mean	11.315	28.87	10.15	0.11	12.595	8.325	21.455	7.185
MDSA	**5.33**	**14.88**	**5.66**	**0.05**	**1.25**	**6.02**	**16.58**	**50.20**

1.3 During the wet season, individual jaguars varied in selection for vegetation types within the study area (second-order selection), but most animals preferred dense and open marshes human-dominated landscapes. Each cell gives the percent of area within 100 m radius of radio-locations for each individual within the Morro do Diabo study area (MDSA).

Animal ID	Water	Prim. Forest	Sec. Forest	Alluvial Forest	Dense Marsh	Open Marsh	Agriculture	Pasture
F1	21.39	5.73	0.07	0.00	6.09	9.53	49.95	7.24
F2	-	-	-	-	-	-	-	-
F3	0.00	96.32	3.53	0.00	0.15	0.00	0.00	0.00
F4	3.15	7.93	7.24	0.00	9.19	38.22	18.46	15.81
F5	-	-	-	-	-	-	-	-
Female Mean	8.18	36.66	3.61	0.00	5.14	15.91	22.80	7.68
M1	11.10	5.62	3.49	0.00	6.50	22.72	37.20	13.37
M2	12.22	42.00	4.01	0.00	36.54	2.87	2.31	0.04
Male Mean	11.66	23.81	3.75	0	21.52	12.79	19.75	6.70
MDSA	**5.33**	**14.88**	**5.66**	**0.05**	**1.25**	**6.02**	**16.58**	**50.20**

1.4 Across wet and dry seasons combined, individual jaguars varied in selection for vegetation types within the home range (third-order selection), but most animals preferred forested areas and avoided human-dominated areas. Each cell gives the percent of area within 100 m radius of radio-locations ("used") or within the 85% fixed kernel home range ("HR") of that animal within the Morro do Diabo study area (MDSA).

Animal	Primary Forest		Sec. Forest		Alluvial Forest		Dense Marsh		Open Marsh		Agriculture		Pasture	
ID	used	HR	used	HR	used	HR	used	HR	used	HR	used	HR	used	HR
F1	18.60	17.80	15.17	18.05	0.26	0.34	5.18	3.96	5.19	3.87	41.56	39.48	5.64	9.86
F2	93.77	82.38	6.03	16.17	0.00	0.02	0.00	0.54	0.00	0.07	0.20	0.54	0.00	0.01
F3	98.24	68.39	1.05	5.29	0.00	0.23	0.41	2.27	0.04	1.39	0.26	3.92	0.00	9.74
F4	2.27	4.73	2.08	3.81	0.07	0.40	2.80	3.96	13.96	17.05	12.28	23.39	61.28	37.69
F5	93.77	82.38	6.03	16.17	0.00	0.02	0.00	0.54	0.00	0.07	0.20	0.54	0.00	0.01
Mean F	61.33	51.14	6.07	11.90	0.07	0.20	1.68	2.25	3.84	4.49	10.90	13.58	13.38	11.46
M1	9.00	10.00	7.00	7.00	0.00	0.00	5.00	7.00	9.00	10.00	28.00	24.00	25.00	21.00
M2	85.00	59.00	2.00	11.00	0.00	0.00	1.00	3.00	0.00	2.00	2.00	5.00	0.00	8.00
Mean M	47.00	34.50	4.50	9.00	0.00	0.00	3.00	5.00	4.50	6.00	15.00	14.50	12.50	14.50

1.5 During the dry season, individual jaguars varied in selection for vegetation types within the home range (third-order selection), but most animals preferred primary and secondary forests and avoided alluvial forests and open marshes. Each cell gives the percent of area within 100 m radius of radio-locations (“used”) or within the 85% fixed kernel home range (“HR”) of that animal within the Morro do Diabo study area (MDSA).

Animal	Primary Forest		Sec. Forest		Alluvial Forest		Dense Marsh		Open Marsh		Agriculture		Pasture	
ID	used	HR	used	HR	used	HR	used	HR	used	HR	used	HR	used	HR
F1	34.43	24.38	18.85	18.63	0.38	0.93	3.97	3.12	0.54	0.88	34.85	41.89	2.14	4.30
F2	93.77	82.38	6.03	16.17	0.00	0.02	0.00	0.54	0.00	0.07	0.20	0.54	0.00	0.01
F3	97.80	70.55	1.35	4.77	0.00	0.20	0.44	2.63	0.05	1.48	0.36	4.21	0.00	8.03
F4	4.48	4.12	3.81	3.86	0.09	0.34	3.06	4.59	15.66	17.34	16.23	22.85	51.37	41.33
F5	93.77	82.38	6.03	16.17	0.00	0.02	0.00	0.54	0.00	0.07	0.20	0.54	0.00	0.01
Mean F	64.85	52.76	7.22	11.92	0.09	0.30	1.49	2.28	3.25	3.97	10.37	14.01	10.70	10.74
M1	7.07	11.42	5.27	7.55	0.14	0.53	5.77	7.20	6.45	9.79	28.32	24.34	28.40	21.53
M2	72.92	60.13	4.26	11.36	0.04	0.16	1.70	2.72	0.88	2.12	3.42	5.29	0.00	8.85
Mean M	39.99	35.77	4.77	9.46	0.09	0.34	3.73	4.96	3.66	5.95	15.87	14.81	14.20	15.19

1.6 During the wet season, individual jaguars varied in selection for vegetation types within the home range (third-order selection), but most animals preferred primary and secondary forests and avoided pastures. Each cell gives the percent of area within 100 m radius of radio-locations (“used”) or within the 85% fixed kernel home range (“HR”) of that animal within the Morro do Diabo study area (MDSA).

Animal	Primary Forest		Sec. Forest		Alluvial Forest		Dense Marsh		Open Marsh		Agriculture		Pasture	
ID	used	HR	used	HR	used	HR	used	HR	used	HR	used	HR	used	HR
F1	10.38	8.26	11.72	10.22	0.00	0.33	2.95	4.65	5.78	7.09	36.99	30.52	16.43	18.37
F3	99.93	60.16	0.01	7.01	0.00	0.18	0.05	1.93	0.00	1.64	0.00	4.71	0.00	12.37
F4	1.89	2.34	3.38	2.36	0.00	0.01	4.89	5.29	23.58	22.72	16.85	22.47	43.30	31.82
Mean F	37.40	23.59	5.04	6.53	0.00	0.17	2.63	3.96	9.79	10.48	17.95	19.23	19.91	20.86
M1	5.62	9.47	3.86	6.23	0.00	0.44	5.28	5.51	9.46	9.81	29.72	25.82	14.79	21.65
M2	78.04	52.21	0.25	9.45	0.00	0.36	2.89	4.10	0.04	4.28	0.09	6.15	0.04	7.62
Mean M	41.83	30.84	2.05	7.84	0.00	0.40	4.08	4.81	4.75	7.04	14.91	15.98	7.41	14.64

1.7 Across both wet and dry seasons, individual jaguars varied in selection for vegetation types within the study area (second-order selection), but most animals preferred dense and open marshes and avoided forested environments. Each cell gives the percent of area within 100 m radius of radio-locations for each individual within the Ivinhema Study Area (ISA)

Animal ID	Water	Prim. Forest	Sec. Forest	Alluvial Forest	Dense Marsh	Open Marsh	Agriculture	Pasture
F1	0.34	0.05	0.72	1.50	13.76	36.34	13.33	33.96
F2	1.33	1.88	3.87	4.15	11.05	40.81	7.41	29.49
Female Mean	0.83	0.96	2.29	2.82	12.40	38.57	10.37	31.72
M1	0.00	0.33	1.80	1.36	5.40	39.41	11.96	39.75
ISA	**5.28**	**1.70**	**3.39**	**2.29**	**4.34**	**18.31**	**14.00**	**50.68**

1.8 During the dry season, individual jaguars varied in selection for vegetation types within the study area (second-order selection), but most animals preferred dense and open marshes and avoided forested environments. Each cell gives the percent of area within 100 m radius of radio-locations for each individual within the Ivinhema Study Area (ISA)

Animal ID	Water	Prim. Forest	Sec. Forest	Alluvial Forest	Dense Marsh	Open Marsh	Agriculture	Pasture
F1	0.67	0.11	1.25	2.26	9.14	54.21	9.94	22.42
F2	1.68	2.37	3.49	5.25	11.63	46.32	8.20	21.06
Female Mean	1.18	1.24	2.37	3.75	10.38	50.27	9.07	21.74
M1	0.00	0.41	2.27	1.71	5.50	46.14	10.54	33.43
ISA	**5.28**	**1.70**	**3.39**	**2.29**	**4.34**	**18.31**	**14.00**	**50.68**

1.9 During the wet season, individual jaguars varied in selection for vegetation types within the study area (second-order selection), but most animals preferred dense, open marshes and avoided forested environments. Each cell gives the percent of area within 100 m radius of radio-locations for each individual within the Ivinhema Study Area (ISA)

Animal ID	Water	Prim. Forest	Sec. Forest	Alluvial Forest	Dense Marsh	Open Marsh	Agriculture	Pasture
F1	0.00	0.00	0.15	0.60	15.10	31.43	14.10	38.62
F2	0.00	0.00	5.12	0.00	9.98	21.36	4.27	59.28
Female Mean	0.00	0.00	2.63	0.30	12.54	26.39	9.18	48.95
M1	0.00	0.00	0.00	0.00	4.94	12.33	18.26	64.46
ISA	**5.28**	**1.70**	**3.39**	**2.29**	**4.34**	**18.31**	**14.00**	**50.68**

1.10 Across wet and dry seasons combined, individual jaguars varied in selection for vegetation types within the home range (third-order selection), but most animals preferred open marshes and pastures and avoided forested areas. Each cell gives the percent of area within 100 m radius of radio-locations (“used”) or within the 85% fixed kernel home range (“HR”) of that animal within the Ivinhema study area (ISA).

Animal	Primary Forest		Sec. Forest		Alluvial Forest		Dense Marsh		Open Marsh		Agriculture		Pasture	
ID	used	HR	used	HR	used	HR	used	HR	used	HR	used	HR	used	HR
F1	0.04	0.48	0.62	2.16	1.19	2.33	8.26	20.05	58.06	33.83	3.18	8.22	28.64	32.90
F2	0.38	1.88	0.82	3.84	2.54	5.70	11.16	13.01	56.36	39.43	1.98	6.41	19.96	22.08
Mean F	0.21	1.18	0.72	3.00	1.86	4.01	9.71	16.53	57.21	36.63	2.58	7.31	24.30	27.49
M1	0.00	0.44	0.58	1.73	1.76	4.16	5.80	15.74	66.81	42.95	3.91	9.17	21.15	25.81

1.11 During the dry season, individual jaguars varied in selection for vegetation types within the home range (third-order selection), but most animals preferred open marshes and pastures and avoided forested areas. Each cell gives the percent of area within 100 m radius of radio-locations (“used”) or within the 85% fixed kernel home range (“HR”) of that animal within the Ivinhema study area (ISA).

Animal	Primary Forest		Sec. Forest		Alluvial Forest		Dense Marsh		Open Marsh		Agriculture		Pasture	
ID	used	HR	used	HR	used	HR	used	HR	used	HR	used	HR	used	HR
F1	0.12	0.62	1.38	2.68	1.86	3.22	10.76	19.28	61.40	36.41	3.78	9.10	20.72	28.41
F2	0.52	2.21	0.39	2.67	3.15	6.90	8.11	11.63	55.15	43.04	2.00	6.33	16.67	18.40
Mean F	0.32	1.41	0.88	2.68	2.51	5.06	9.43	15.45	58.28	39.72	2.89	7.72	18.70	23.41
M1	0.00	0.92	0.37	1.60	1.35	4.06	3.16	16.12	74.59	41.75	1.92	8.10	18.61	27.46

1.12 During the wet season, individual jaguars varied in selection for vegetation types within the home range (third-order selection), but most animals preferred open marshes and pastures and avoided forested areas. Each cell gives the percent of area within 100 m radius of radio-locations ("used") or within the 85% fixed kernel home range ("HR") of that animal within the Ivinhema study area (ISA).

Animal	Primary Forest		Sec. Forest		Alluvial Forest		Dense Marsh		Open Marsh		Agriculture		Pasture	
ID	used	HR	used	HR	used	HR	used	HR	used	HR	used	HR	used	HR
F1	0.00	0.10	0.18	0.88	0.85	1.26	10.69	20.15	36.98	32.49	3.77	8.45	47.53	36.67
F2	0.00	1.25	3.97	8.09	0.00	0.84	8.90	12.90	28.24	29.74	2.64	8.09	56.25	37.43
Mean F	0.00	0.67	2.07	4.49	0.43	1.05	9.80	16.53	32.61	31.11	3.20	8.27	51.89	37.05
M1	0.00	0.01	0.00	0.04	0.00	0.01	2.36	7.15	27.55	16.21	10.85	17.63	59.24	58.96

Appendix 2. Pictures

Plate 1. The Morro do Diabo (Devil's Hill) State Park and the road bisecting this protected area (37.000 ha).

Plate 2. The Paranapanema River, in the south of Morro do Diabo. Across de River is the State of Parana and the Copacabana Farm where some jaguars established their core areas.

Plate 3. Copacabana Farm, around Morro do Diabo, considered am “easy prey” area for some study animals.

Plate 4. Land reform settlements in the west border of Morro do Diabo State Park.

Plate 5. Gallery forests used as corridors and stepping stones for jaguars during their long movements.

Plate 6. Female jaguar and her cub captured in the Copacabana Farm in the edge of Morro do Diabo State Park.

Plate 7. Veterinarian Alessandra Nava taking blood samples from a male jaguar captured in a box trap in Morro do Diabo State Park.

Plate 8. The author, with a female jaguar captured in Ivinhema State Park.

Plate 9. The jaguar hunter Carlos Plateiro withhis hounds and field assistants in Ivinhema State Park.

Plate 10. The field team in Ivinhema State Park.

Plate 11. The jaguar hunter, Carlos Plateiro with male and female jaguars captured in Ivinhema State Park.

Plate 12. A Marsh Deer (*Blastocerus dichotomus*) in the open marshes of Ivinhema State Park.

Plate 13. Aerial monitoring around Morro do Diabo State Park.

Plate 14. Downloading jaguar locations from the receptor to the computer. In the left, pictures from camera traps in the Morro do Diabo State Park.

Plate 15. Female and cub photographed during field work in Ivinhema State Park.

Plate 16. Radio tracked male jaguar crossing the Ivinhema River.

Plate 17. Agroforestry systems implemented with local settlers around Morro do Diabo State Park.

Plate 18. Agroforestry community nursery implemented around Morro do Diabo State Park