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Assessing the Viability of Lowland Tapir Populations in a Fragmented Landscape

By

Emília Patrícia Medici

Thesis submitted for the degree of
Doctor of Philosophy
in Biodiversity Management
Durrell Institute of Conservation and Ecology (DICE)
University of Kent
Canterbury, United Kingdom
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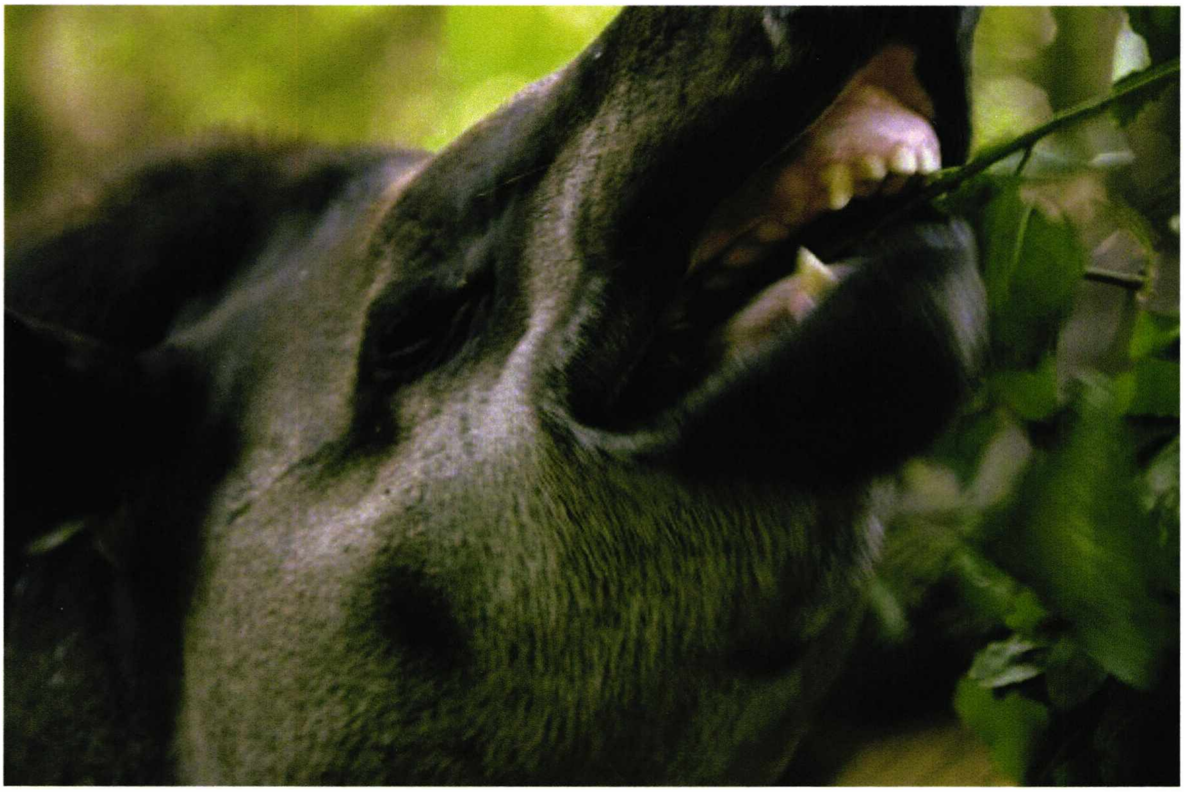
To Dr. Maurício Pompilio, Dr. José Tadeu dos Santos and
the entire staff of Clínica Campo Grande for saving
my husband's life and ultimately allowing
me to finish this thesis ...

... and to the tapirs of the Atlantic Forest ...



Abstract

This thesis aimed to assess the ecological factors that determine the long-term persistence and viability of animal populations across severely fragmented landscapes. The lowland tapir, *Tapirus terrestris*, and the fragmented Atlantic Forests of the Interior of the Pontal do Paranapanema Region, São Paulo State, Brazil, were used as a model to illustrate this assessment. Both empirical and modelling approaches were used. The empirical approach focused on aspects of tapir spatial ecology, intra-specific interactions, spatial and temporal interactions between tapirs and the landscape, as well as estimates of tapir abundance in Morro do Diabo State Park (370 km^2) and seven smaller forest fragments (4-18 km^2) where tapirs were present. The modelling approach consisted of a Population Viability Analysis (PVA) using the software VORTEX. Spatial ecology, intra-specific interactions, and interactions between tapirs and the landscape were estimated by radio-telemetry. Population sizes were derived from tapir densities obtained by radio-telemetry, nocturnal line-transect sampling, and Footprint Identification Technique (FIT). Lowland tapirs in Morro do Diabo had very large home ranges (4.7 km^2) when compared to other sites, particularly contiguous habitats. Tapir home ranges had very complex internal structures, including multiple core areas of use, which comprised a very small proportion of the home range (50% core area, 17% of the home range; 25% core area, 6% of the home range). Little seasonal variation in size and location of home ranges and core areas of use were observed. These patterns were consistent for both sexes and different age classes. Telemetry results have shown that a minimum of 20 months of data collection and approximately 300 locations are necessary to determine home range size for adult lowland tapirs. Tapirs exhibited extensive home range overlap (30%), as well as overlap of core areas of use (20%). No evidence of spatial territoriality was noted. Tapirs incorporated portions of all available habitat types within their home ranges and core areas of use, but significantly selected riparian habitats, where they performed most of their main activities, particularly foraging. Tapirs avoided areas of agricultural and pastoral land, as well as secondary growth forests. It was estimated that Morro do Diabo hosts a population of 130 tapirs and, altogether, the seven forest fragments host 22 additional individuals. Tapirs have low population growth rates and so are very susceptible to threats such as road-kill, infectious disease, and fire, particularly in the small forest fragments. Results from the PVA model projected that the tapir population in Morro do Diabo has zero probability of extinction and is likely to persist over the next 100 years. However, the population is not large enough to maintain 95% of genetic diversity over the long-term. A Minimum Viable Population of 200 tapirs would be required to ensure long-term viability. The model showed that, without dispersal of tapirs from Morro do Diabo, tapirs in the small fragments will go extinct over the next 100 years. However, this study showed that tapirs in the Pontal do Paranapanema Region moved fairly easily through areas of non-natural habitat in between patches of forest, indicating a certain level of landscape functional connectivity. This provided evidence of a tapir metapopulation scenario, which proved to be a determinant factor for the persistence and viability of lowland tapirs in the Atlantic Forest of the Interior. Overall, the long-term persistence and viability of animal populations across severely fragmented landscapes appears to be dependent on the maintenance and full protection of complex landscape networks. These networks must include some large patches of habitat that can host larger animal populations and function as source areas for dispersal of individuals to smaller populations in sink habitats. Patches of forest comprising these networks must incorporate required habitat types where animals can find the resources they need in order to survive and persist. Most essentially, there must be an appropriate level of landscape connectivity, either structurally or functionally, in order to facilitate biological fluxes between patches and promote the maintenance of a demographically and genetically healthy metapopulation.

Resumo

Esta tese teve como meta principal avaliar os fatores ecológicos determinantes para a persistência e viabilidade de populações animais em paisagens severamente fragmentadas no longo prazo. A Anta Brasileira, *Tapirus terrestris*, e a Floresta Atlântica do Interior da região do Pontal do Paranapanema, São Paulo, Brasil, foram utilizadas como modelos ilustrativos para esta avaliação. Duas abordagens foram utilizadas, a primeira delas empírica e a segunda baseada em modelagem. A abordagem empírica avaliou aspectos de ecologia espacial, interações intra-específicas e interações espaciais e temporais entre as antas e a paisagem, bem como estimativas de abundância no Parque Estadual Morro do Diabo (370 km^2) e sete outros fragmentos de floresta (4-18 km^2) onde a presença da espécie havia sido previamente confirmada. A modelagem consistiu de uma Análise de Viabilidade Populacional (AVP) realizada através do uso do software VORTEX. Parâmetros de ecologia espacial, interações intra-específicas e interações entre antas e paisagem foram estimados através de rádio-telemetria. Tamanhos populacionais foram derivados a partir de densidades obtidas através de rádio-telemetria, censo noturno por transectos lineares, e uma técnica de identificação de pegadas (FIT). As antas no Morro do Diabo apresentaram áreas de uso (*home range*) bastante grandes (4,7 km^2) quando comparadas a outras áreas, em particular em florestas contínuas. As áreas de uso apresentaram estruturas internas complexas, incluindo múltiplos centros de alta intensidade de uso (*core areas*), os quais representaram proporções bastante pequenas da área de uso total (50% core, 17% da área de uso; 25% core, 6% da área de uso). Pouca variação sazonal foi encontrada tanto em tamanho quanto em localização de áreas de uso e áreas core. Todos esses padrões foram consistentes para ambos os sexos e diferentes classes de idade. Resultados de telemetria mostraram ser necessários um mínimo de 20 meses de coleta de dados e aproximadamente 300 localizações para determinar a área de uso de antas adultas. As antas tiveram alta sobreposição de área de uso (30%), bem como de áreas core (20%). Territorialidade não foi observada. As antas incorporaram em suas áreas de uso e áreas core porções de todos os tipos de habitat disponíveis, mas selecionaram significativamente florestas ripárias, onde pareceram executar grande parte de suas atividades, particularmente forrageamento. As antas evitaram áreas de agricultura e pastagem, bem como florestas secundárias. A população de antas no Morro do Diabo foi estimada em 130 indivíduos e os sete outros fragmentos de floresta, conjuntamente, devem conter cerca de 22 outros indivíduos. A taxa de crescimento populacional da espécie é baixa e, conseqüentemente, as antas são bastante susceptíveis a ameaças tais como atropelamentos, doenças infecciosas e fogo, particularmente em fragmentos de menor tamanho. Os resultados do modelo de AVP projetaram que a população de antas no Morro do Diabo tem zero probabilidade de extinção e deve persistir ao longo dos próximos 100 anos. Entretanto, a população não é suficientemente grande para manter 95% de diversidade genética no longo prazo. Seria necessária uma População Mínima Viável de 200 antas para garantir a viabilidade no longo prazo. O modelo demonstrou que na ausência de dispersão de indivíduos do Morro do Diabo, as populações de antas nos fragmentos menores serão extintas ao longo dos próximos 100 anos. Todavia, este estudo mostrou que as antas apresentaram relativa facilidade em se deslocar pela matriz da paisagem entre os fragmentos, indicando certo nível de conectividade funcional. Isso evidenciou um cenário metapopulacional, o qual provou ser determinante para a persistência das antas na Floresta Atlântica do Interior. De maneira geral, a persistência e viabilidade de populações animais em paisagens severamente fragmentadas parecem depender da manutenção e proteção de complexas networks de habitat. Tais networks devem incluir alguns fragmentos de maior tamanho que possam dar suporte a populações maiores e funcionar como fontes de dispersores para pequenas populações em habitats sumidouro. Os fragmentos de floresta compondo essas networks devem incorporar os tipos de habitat requeridos onde os animais possam encontrar os recursos necessários para sua sobrevivência e persistência. Mais importante, deve haver um nível apropriado de conectividade de paisagem, seja ela estrutural ou funcional, de forma a facilitar fluxos biológicos entre os fragmentos e promover a manutenção de uma metapopulação saudável tanto em termos demográficos quanto genéticos.

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Chapter 1

General Introduction

&

Thesis Aims and Structure

Photo by Rolex Awards

1.1 General Introduction

Worldwide, natural habitats are increasingly threatened by escalating human population and the resulting conversion for agriculture and urban development (Vitousek *et al.* 1997). Habitat loss and fragmentation are considered to be the primary causes of the present extinction crisis (Wilcox & Murphy 1985; Gibb & Hochul 2002; Schmiegelow & Monkkonen 2002; Vié *et al.* 2009). The underlying question posed by this thesis is: What are the ecological factors that determine the long-term persistence and viability of animal populations across severely fragmented landscapes? I used the lowland tapir, *Tapirus terrestris*, living in the Atlantic Forests of the Interior of the Pontal do Paranapanema Region, São Paulo State, Brazil, as a model to illustrate and answer this question.

1.1.1 Habitat Fragmentation

Habitat fragmentation is defined as "the simultaneous reduction of the area of a focal habitat and increased isolation of the remaining habitat patches with a net habitat loss" (Saunders *et al.* 1991). Fragmented ecosystems usually fail to provide the necessary resources to support species assemblages found in the intact ecosystem, in turn leading to a general reduction in the abundance of species (Lovejoy *et al.* 1984; Quinn & Hastings 1987; Bierregaard *et al.* 1992; Burkey 1993; Kattan & Alvarez-Lopez 1996). The process of habitat fragmentation involves several factors, which have serious repercussions on plant and animal species that originally occupied large contiguous areas of wild habitat (Schmiegelow & Monkkonen 2002; Gehring & Swihart 2003). Fragmentation can exacerbate the effects of pure habitat loss potentially producing population declines at landscape scales (Andren 1994; Bender *et al.* 1998). This may result in population extinctions even if suitable habitat still exists. In addition to causing immediate local extinctions, fragmentation may have long-term effects on populations through changes in ecological processes such as pollination, predation, use of space, territorial behaviour, and feeding habits. Moreover, microclimatic consequences of fragmentation, such as changes in solar radiation, humidity and wind pattern, are detrimental to many organisms (Laurance 1991; Laurance 1994; Young & Mitchell 1994). Lastly, by opening core areas, fragmentation of contiguous habitat patches leads to a dramatic increase in edges in the landscape, which provides distinct microclimatic conditions from the core and may become less suitable for some species (Sih *et al.* 2000).

Ultimately, habitat fragmentation results in the geographic isolation of "habitat islands" among a matrix of urban or agricultural land uses. The mobility of some organisms might thus become restricted thereby isolating populations (Andreassen *et al.* 1996; Vos *et al.* 2001). As the isolation of habitat fragments increases, the probability of their recolonisation decreases (Parker & MacNally 2002). The contention that small, isolated populations are more vulnerable to extinction through stochastic processes has a sound theoretical basis in both demography and population genetics (Shaffer 1981; Lande 1988; Roelke *et al.* 1993). Small populations are more sensitive to stochastic events, such as fires or epidemic outbreaks, which can rapidly drive a population to extinction (Lacy 1993; Lacy 2000; Aurambout *et al.* 2005). Likewise, isolated populations are more susceptible to genetic drift, which can also lead, in the case of severe inbreeding, to population extinctions (Templeton *et al.* 1990). The chance of extinction increases exponentially with decreasing population size and increasing population isolation.

Conservationists around the world are increasingly going to be called upon to mastermind rescue operations designed to manage and conserve wildlife species in severely fragmented landscapes, and they must be prepared for this undertaking. More than ever, there is a pressing need to understand how animal populations cope with the past and current patterns of habitat loss and fragmentation, and what these populations require in order to persist and be viable over the long-term.

1.1.2 Long-Term Viability of Animal Populations

Concern about the long-term persistence of animal populations (Smith 1974; Shaffer & Sampson 1985; Goodman 1987; Newmark 1987) has led to questions about the ecological requirements and the size a population should be to increase its chances of survival and minimise its chances of extinction (Gilpin & Diamond 1980; Wilcox & Murphy 1985). Some qualitative factors of population persistence include the existence of suitable habitats largely connected, large habitat areas, high reproductive rates, and environmental conditions that increase habitat carrying capacity and population growth rates (Ruggiero *et al.* 1994). Thus far, only evidence from simulation models (Diamond 1984; Harris *et al.* 1987; Iwasa & Mochhizuki 1988; Lacy 1993; Lacy 2000) and of the historical loss of species of unknown population sizes (Brown 1971; Patterson 1984) has been available to suggest how long fragmented animal populations might persist. However, it has generally not been possible to assess empirically the generality of these models or the appropriateness of conservation strategies (Lande 1988). Neither the timeframe of persistence in relation to population size, nor the effects of various factors are well understood. As entire biomes continue to be destroyed and fragmented, and questions arise about the ecological requisites to assure the persistence of many species, empirical assessments of the viability of animal populations become increasingly important.

The viability of a population is the probability that this population will persist for some specified period of time (White 2000). The viability of animal populations is usually evaluated quantitatively. The procedures commonly used include the estimation of Minimum Viable Populations (MVP) and Population Viability Analysis (PVA). Minimum Viable Population is the smallest population size that will persist for some specified length of time with a specified probability (Shaffer 1981). Population Viability Analysis evaluates the probability of a population of a specified size declining or going extinct over a specified length of time (Gilpin & Soulé 1986; Boyce 1992; Lacy 2000; Clark *et al.* 2002). For both MVP and PVA, the definitions and criteria for viability, persistence, and extinction are set as arbitrary targets, such as a 95% probability of a population persisting for 100 years (Boyce 1992).

In this thesis, I used two different approaches to assess the long-term persistence and viability of lowland tapir populations in the Atlantic Forest fragments of the Pontal do Paranapanema Region. The first approach was based on the empirical information obtained for the species during this study. This empirical approach focused on aspects of tapir spatial ecology and intra-specific interactions, spatial and temporal interactions between tapirs and the landscape, as well as estimates of tapir abundance, which are all determinant factors for persistence and viability. The second approach consisted of modelling tapir population viability, using a computer simulation known as Population Viability Analysis. This modelling approach was based on biological characteristics of the species including reproductive and mortality rates. The PVA process produced an estimate of the probability of extinction, and of minimum viable population size for long-term viability, as well as the analysis of the impact of threats and management scenarios. The results from both the empirical and modelling approaches were used to substantiate the discussion of management and conservation strategies that should be implemented in order to reduce the risk of extinction of lowland tapir populations, and therefore promote their long-term persistence and viability in the Atlantic Forests of the Pontal do Paranapanema Region.

1.1.3 Why is the tapir a good model?

The lowland tapir was considered to be a suitable model for this assessment because of the various particular intrinsic and extrinsic biological aspects of the species. Regarding intrinsic aspects, the most important are life-history characteristics, spatial and habitat requirements, as well as the role played in the ecological functioning of ecosystems. In terms of extrinsic aspects, the most critical ones for tapirs in the Atlantic Forest are inter-specific competition and predation, both factors that are important in population regulation (Dublin *et al.* 1990; Sinclair 2003).

The lowland tapir is the second largest terrestrial mammal in South America, the first being the Baird's tapir (*Tapirus bairdii*). Tapir populations do not easily recover after a severe reduction, and can rapidly be driven to extinction. Tapirs are what was formerly called K-selected species, but are now considered to be "slow species" in the "fast-slow continuum" of life-histories (MacArthur & Wilson 1967; Dobson & Oli 2007). Slow species have large body size, long life span, and produce fewer offspring that require high levels of parental care until they mature. Populations of slow species tend to be maintained at carrying capacity. In addition, tapirs have very low reproductive rates. Females do not become sexually mature until they are nearly 2 years of age (Eisenberg 1997), and they produce a single offspring after a lengthy gestation of 13-14 months (Barongi 1993). Lastly, tapirs have a long generation length, estimated to be between 11-15 years (Medici *et al.* 2007a; IUCN 2008a). Given these life-history characteristics, tapir populations do not attain high levels of local abundance and are particularly susceptible to habitat fragmentation. Furthermore, while habitat fragmentation leads to small populations, other threats such as hunting, road-kill, and disease among others override the impact of fragmentation strongly impacting the likelihood of extirpation of remaining tapir populations (Bodmer *et al.* 1997). All this makes the tapir an appropriate candidate for the purpose of this assessment.

Tapirs are wide-ranging species. Home range area and body mass are positively correlated for most animal feeding styles and seasons (McNab 1963; Mysterud *et al.* 2001). Large terrestrial mammals - such as tapirs - have larger home ranges and a greater absolute mobility than do small mammals (Eisenberg 1980). While the spatial requirements of tapirs vary with the carrying capacity of different habitats found within their distribution range (Eisenberg 1997; Medici *et al.* 2007a), they usually require considerably large home ranges (Williams 1978; Williams 1984; Foerster 1998; Herrera *et al.* 1999; Foerster & Vaughan 2002; Noss *et al.* 2003; Ayala 2003; Lizcano & Cavelier 2004; Tobler 2008; Abdul Ghani 2009; Naranjo 2009). This is particularly important for the persistence of tapirs in fragmented habitats, given that species with large spatial requirements generally cannot find sufficient food or other vital resources to survive over the long-term in a smaller area (McNab 1963; Redford & Robinson 1991). Chiarello (1999) analysed the effects of the Atlantic Forest fragmentation on mammal communities, and observed that tapirs were present in larger patches but not recorded in the smaller forest fragments. In addition to large home range sizes, tapirs have complex home range structures, with multiple core areas of use (Tobler 2008) that are established according to the distribution of patches of preferred habitat types. Moreover, tapir species exhibit extensive home range overlap (Foerster & Vaughan 2002; Ayala 2003; Noss *et al.* 2003), which is a determinant factor for tapir spatial territoriality and intra-specific interactions. Ensuring the long-term persistence of a species with large, complex spatial requirements also promotes the survival and persistence of other species living in the same area.

Population size is a critical demographic attribute and the most important parameter to determine extinction risk (Shaffer 1981; Gilpin & Soulé 1986; Lacy 1993; Lacy 2000; Shaffer *et al.* 2000; Aurambout *et al.* 2005). Whereas controversy remains as to how large populations need to be to ensure the viability of a given species over the long-term (Reed & Hobbs 2004), population size is considered to be the major determinant of viability for a variety of animal species (Newmark 1987; Pimm *et al.* 1988; Richman *et al.* 1988; Soulé *et al.* 1988; Berger 1990; Schoener & Spiller 1992; Foufopoulos & Ives 1999). Lowland tapir population density tends to be low. Estimates range from a relatively high of 1.6 tapirs km^{-2} in Neotropical forests in undisturbed, non-hunted, or lightly hunted sites (Robinson & Redford 1986; Robinson & Redford 1991) to less than 0.3 tapirs km^{-2} in different regions and habitats where they occur (Cullen *et al.* 2000; Aquino *et al.* 2001; Aquino & Calle 2003; Haugaasen & Peres 2005; Desbiez 2009). Ensuring the persistence of a species which occurs at low density in a severely fragmented habitat is considerably more challenging than doing so for a species which occurs at higher densities.

The lowland tapir has a broad geographic distribution (Hershkovitz 1954; Emmons & Feer 1997; Eisenberg 1997), and seems to be adapted to a wide range of habitat types (Medici *et al.* 2007a; Taber *et al.* 2008). In spite of that, a number of studies have identified patterns of habitat preference and selection in tapir species (Bodmer 1990b; Fragoso 1991a; Fragoso 1991b; Naranjo 1995; Salas 1996; Foerster 1998; Naranjo & Cruz-Aldán 1998; Herrera *et al.* 1999; Foerster & Vaughan 2002; Ayala 2003; Lizcano 2006; Tobler *et al.* 2006; Tobler 2008; Steinmetz *et al.* 2008). There is growing evidence that besides large home ranges, tapirs also require certain habitat types that contain the resources they need or prefer in order to persist over the long-term. Thus, ensuring the persistence and viability of lowland tapir populations over the long-term requires the protection of habitat integrity and diversity, which will in turn benefit a number of other species.

Forest reduction and fragmentation are generally accompanied by a loss of habitat diversity, which in turn affects resource diversity (Wright & Duber 2001; Tabarelli *et al.* 2004). While tapirs are essentially browsers, they consume fruit extensively when available (Bodmer 1991b; Fragoso & Huffman 2000; Henry *et al.* 2000; Salas & Fuller 1996; Tobler 2008). There is growing evidence that the availability of fruit in small forest fragments is lower than that in continuous tracts of tropical forest (Terborgh 1986; Terborgh 1992). As a consequence, some frugivores will emigrate from these areas during periods of fruit scarcity, while others may alter their diets (Lovejoy *et al.* 1986; Terborgh 1986; Rylands & Keuroghlian 1988). In general, decreased fruit productivity will reduce the viability of frugivore populations in forest fragments (Wright *et al.* 1999; Fleury & Galetti 2004; Keuroghlian & Eaton 2008). A suite of resource-related factors specific to different habitat types, such as the spatial distribution of fruit sources, total fruit availability, seasonal fruit availability, and severity of fruit scarcity periods, will affect habitat use, area requirements, and ultimately the persistence of frugivore populations in habitat fragments (Keuroghlian & Eaton 2008). Tófoli (2006) analysed the impact of fragmentation of the Atlantic Forests of the Pontal do Paranapanema Region on the diet of lowland tapirs and showed that tapirs in Morro do Diabo State Park, the largest forest remnant in the Pontal do Paranapanema Region, consumed significantly higher percentages of fruit and lower percentages of fibrous material when compared with tapirs in the smaller forest fragments of the Pontal do Paranapanema Region. In addition, estimates of fruit species richness in the diet of tapirs indicated a considerably higher diversity in Morro do Diabo than in the forest fragments (Tófoli 2006). Thus, it is evident that habitat fragmentation has had an effect on the diet of tapirs, negatively affecting the tapir populations in small forest fragments. Lowland tapirs are therefore an excellent candidate to illustrate the impacts of decreasing resources due to fragmentation.

Due to the combination of all factors described above, tapirs are widely recognised as "umbrella species". Umbrella species are "species with large area requirements, which if given sufficient protected habitat area, will bring many other species under protection" (Noss 1990; Caro & O'Doherty 1999; Entwistle & Dunstone 2000; Caro 2003). In other words, meeting the needs of an umbrella species will provide protection for the species with which they co-occur and the natural habitats on which they all depend. Determining the ecological requirements that will ensure the long-term persistence of an umbrella species population in a severely fragmented landscape will also ensure the long-term persistence of many other species.

Tapirs are also considered to be "landscape species", *i.e.* "species that occupy large home ranges often extending beyond protected area boundaries, that require a diversity of ecosystem types, and that have a significant impact on the structure, productivity and resilience of natural ecosystems" (Sanderson *et al.* 2002; Coppolillo *et al.* 2003). Exclusion experiments carried out with large terrestrial herbivores in Bolivia have demonstrated that lowland tapir, white-lipped peccary (*Tayassu pecari*), collared peccary (*Tayassu tajacu*), grey-brocket deer (*Mazama gouazoubira*), and red-brocket deer (*Mazama americana*) affect ecosystem dynamics in different ways (Painter 1998). Generally speaking, these animals impact the structure and diversity of plant communities by decreasing the abundance of preferred species (Bazely & Jefferies 1986; Virtanen *et al.* 1997; Olofsson 2001; Brathen & Oksanen 2001; Grellmann 2002), and by changing competitive interactions between plants (Virtanen 1998; Mulder & Ruess 1998; Olofsson *et al.* 2002), therefore maintaining habitat heterogeneity (Terborgh 1988; Dirzo & Miranda 1991). The relative impact of herbivores is a function of body size (Demment & Van Soest 1985; Freeland 1989; Olff & Ritchie 1998). Large animals such as tapirs, even at low population densities, can comprise a significant biomass and consume large amounts of food. Foerster (1998) estimated that Baird's tapirs consumed an average of 16 kg of fruit and fibrous materials per day. In addition, tapirs selectively browse vegetative parts of different food plants (Salas & Fuller 1996), and seem to play an important role as long-distance seed dispersers (Janzen 1981; Eisenberg 1990; Bodmer 1991b; Rodrigues *et al.* 1993; Henry *et al.* 2000; Galetti *et al.* 2001; Fragoso *et al.* 2003). The pattern of movements of tapirs affects seed shadows by determining where seeds are dispersed and in what amount, and the intensity of predation to which they are subjected

(Fragoso 1994). Tapirs ingest whole seeds and either spit or drop large numbers of viable seeds within their faeces (Varela & Brown 1995; Painter & Rumiz 1999). These seeds may experience lower rates of predation than seeds not in faeces, which suggest that tapirs may increase the effectiveness of seed dispersal if they deposit faeces away from parent plants (Fragoso 1994; Olmos *et al.* 1999). Bodmer (1991b) found that the lowland tapir is the only ungulate that regularly disperses seeds in the Amazon. Lowland tapirs are especially important for the dispersal of seeds of some palm trees, such as *Syagrus romanzoffiana* in the semi-deciduous Atlantic Forest (Olmos *et al.* 1999). Fragoso (1997) anticipated that the reproductive success and distribution of *Mauritia maripa* palm in the Amazon was due largely to tapirs. Lastly, tapir seed dispersal also allows for secondary dispersal by small rodents that remove the seeds deposited by tapirs in latrines (Fragoso 1994; Fragoso 1997). Tapirs are not ruminants, they have a hypertrophic cecum and, consequently, seed predation by digestion is lower when compared to other large-sized mammalian herbivores, such as deer and peccaries (Janzen 1981; Bodmer 1991b; Fragoso *et al.* 2003). For all these reasons, tapirs play a critical role in shaping the structure and maintaining the functioning of ecosystems, and thus have been recognised as "ecological engineers" (Fragoso 1998) as well as "gardeners of the forest" (Painter 1998). Therefore, local tapir extinctions or drastic population declines may trigger a breakdown of key ecological processes, eventually jeopardising the integrity of the ecosystem over the long-term (Foerster & Medici 2002; Medici *et al.* 2007a). Determining the ecological factors that will ensure the long-term persistence of a landscape species will ensure the ecological integrity of the ecosystem.

Landscape species use a variety of habitats and their movements can functionally link different habitat types or regions within a given landscape (Sanderson *et al.* 2002). Large animals likely have a greater perceptual range (Zollner 2000), thereby influencing the detection of suitable habitat and the perception of landscape structure and interrelatedness (Wiens 1996). Therefore, the elimination of a landscape species may undermine these functional links between different habitats and lead to cascading changes in ecological communities or even the loss of the ecosystem functions critical to the persistence of other species, communities, and the larger landscape itself (Sanderson *et al.* 2002). The use of the umbrella and landscape species concepts have been advocated as efficient tools for identifying priority areas in need of protection (Shafer 1990; Sanderson *et al.* 2002; Caro 2003).

In addition to lowland tapirs, the community of large herbivores of the Atlantic Forests of the Pontal do Paranapanema Region includes the white-lipped peccary (*Tayassu pecari*), collared peccary (*Tayassu tajacu*), grey-brocket deer (*Mazama gouazoubira*), and red-brocket deer (*Mazama americana*). These five species are sympatric throughout most of their ranges. They all have broad diets including fruit, browse and fibre in different proportions (Bodmer 1991b; Gayot *et al.* 2004; Beck 2005; Tobler 2008). Bodmer (1991a) studied resource partitioning among these five species in the Peruvian Amazon, and analysed the diet and habitat use of all five species concluding that each species partitioned at least one resource type from every other species. In another site of the Peruvian Amazon, Tobler *et al.* (2009) observed a high spatial overlap among these five species, and claims that diet was the most important factor in resource partitioning among them. Even though Tobler *et al.* (2009) observed an apparent competition for fruit, the high diversity and spatial distribution of plant species in the Amazon appeared to allow for enough variation in their diet to permit the five species to coexist. Nevertheless, this might be different in fragmented landscapes. When compared to continuous tracts of forest, fragmented landscapes have lower fruit diversity (Wright & Duber 2001; Tabarelli *et al.* 2004), as well as lower fruit availability (Terborgh 1986; Terborgh 1992), which can potentially lead to a disruption of natural patterns of inter-specific competition.

Inter-specific competition is one of the major selective forces causing the differential use of resources (Schoener 1986), and population regulation (Dublin *et al.* 1990; Sinclair 2003), therefore playing an important role in the structure of ecological communities (Connell 1983; Schoener 1983; Schoener 1984; Maurer 1985; Goldberg & Barton 1992; Gurevitch *et al.* 1992). The theory of community ecology predicts that resource partitioning, fluctuations in population densities, and responses to changes in environmental factors in space and time will have major effects on species coexistence (Chesson 2000; Simberloff 2004; Chase 2005; Guisan & Thuiller 2005; Sinclair & Byrom 2006). Inter-specific competition for food resources on herbivore assemblages arises whenever one species reduces shared food resources below the level that can be exploited efficiently by other species (Tokeshi 1999; Murray & Illius 2000). Instead, by reducing plant biomass, one species may benefit others by facilitating access to forage of a suitable height or quality (Gordon 1988; McNaughton *et al.* 1997), or the quality of eventual re-growth may be higher (Alpe *et al.* 1999; Arsenault & Owen-Smith 2002). Disrupted patterns of inter-specific competition could potentially lead to rapid demise of small tapir populations and have consequences on the community of frugivores with which it shares several niches.

Lowland tapirs are part of the prey base of jaguars (*Panthera onca*) and pumas (*Puma concolor*) in the Atlantic Forests of the Pontal do Paranapanema Region. However, tapirs are not the primary food source for these large cats, which prefer small- to medium-sized preys (Polisar *et al.* 2003; Astete *et al.* 2008). In addition, tapirs occur at low population densities, so making it difficult for predators to encounter them. Nevertheless, a few studies have recorded tapir predation by jaguar (Taber *et al.* 1997; Garla *et al.* 2001; Astete *et al.* 2008). Furthermore, tapir predation was observed on several occasions during this study. Three out of 25 radio-collared tapirs were predated by either jaguar or puma, while I found three carcasses of non-tagged tapirs killed by jaguars. Thus, tapir predation should be considered as one of the components of tapir population regulation, especially when considering small, isolated populations in fragmented habitats. Fragmented landscapes can exacerbate the effect of predation on prey population dynamics by allowing carnivores to concentrate their hunting efforts on islands of preferred prey habitat (Wirsing *et al.* 2002). Likewise, edge habitats resulting from fragmentation also contribute to higher predation rates by favouring generalist predator influx (Schmiegelow & Monkkonen 2002).

For all the reasons described, the tapir is a suitable species to be used as a tool for the assessment of long-term persistence and viability of animal populations across fragmented landscapes. The evaluation of the ecological requirements of tapir populations in the fragmented landscape of the Pontal do Paranapanema Region should provide critical information for the evaluation of the current status of these populations, as well as for the understanding of how tapirs were affected by the past process of habitat loss and fragmentation. Furthermore, this information should allow for the assessment of the ability of tapirs to survive and persist in fragmented landscapes over the long-term.

1.1.4 Why is the Atlantic Forest of the Interior a good model?

Habitat fragmentation is a worldwide phenomenon, and the ecologically complex tropical rain forests have been one of the prime targets (Wilcove *et al.* 1986; Skole & Tucker 1993; Cuarón 2000). Amazonian forests are experiencing rapid and unprecedented changes due to deforestation and habitat conversion, and these changes are having major impacts on wildlife, regional hydrology and the global climate (Laurance 2005; Perz *et al.* 2005). Likewise, the Atlantic Forest biome has suffered large-scale habitat destruction and fragmentation for the past 500 years (Ribeiro *et al.* 2009). The loss of the Atlantic Forest biome has been widely acknowledged as one of the most alarming conservation issues in the world (Mori *et al.* 1981; Terborgh 1992; Viana *et al.* 1997).

In historical times, the Atlantic Forest biome stretched almost continuously for 4,000 km along the eastern Brazilian coast from Rio Grande do Norte at the easternmost tip of the South American continent to as far as Rio Grande do Sul, the southernmost Brazilian state (Eiten 1970; Collins 1990; Dean 1997; Morellato & Haddad 2000; SOS Mata Atlântica & INPE 2008), extending inland into eastern Paraguay and north eastern Argentina. The original extent of the Atlantic Forest in the three countries of occurrence was estimated to be ~1.5 million km^2 (Sanjurjo & Gauto 1996; Cartes 2003; Giraudo *et al.* 2003; Ribeiro *et al.* 2009). Today, this biome has been reduced to ~88% of its original size (Ribeiro *et al.* 2009). Atlantic Forests were largely and rapidly converted to anthropogenic systems (Brown & Brown 1992; Coimbra-Filho & Câmara 1996; Dean 1997). The Atlantic Forest was cleared mainly for timber, firewood, charcoal, agriculture, cattle ranching, and the construction of cities (Morellato & Haddad 2000). The remaining Atlantic Forest consists of small and isolated forest islands scattered across a landscape dominated by agricultural uses and urban development and are still under severe pressure, suffering from various patterns of habitat fragmentation (Morellato & Haddad 2000).

The Atlantic Forest domain can be subdivided into two major regions based on vegetation types and geographical features (Mori *et al.* 1981; Morellato & Haddad 2000). The first vegetation type is classified as Tropical Evergreen Mesophytic Broadleaf Forest or Atlantic Rain Forest. The second is the Tropical Semi-Deciduous Mesophytic Broadleaf Forest or Atlantic Semi-Deciduous Forest, also known as Atlantic Forest of the Interior. The Atlantic Rain Forest covers mostly the low to medium elevations (≤1,000 m) of the eastern slopes of the mountain chain that runs along the coastline from southern to north eastern Brazil (Eiten 1970). The Atlantic Semi-Deciduous Forest extends across the western range of the coastal hills, stretching to the *Plateau* region (≥600 m) in the centre and south eastern interior of Brazil and stretching into Paraguay and Argentina (Leitão-Filho & Morellato 1997; Oliveira-Filho & Fontes 2000). This lowland tapir study took place in the Atlantic Forest of the Interior.

Nowadays, only 2% of the Brazilian Atlantic Forest of the Interior still remains (Dean 1997; SOS Mata Atlântica & INPE 2008). Some of the most significant remnants of these forests are found in the *Plateau* region of Brazil (SOS Mata Atlântica & INPE 2008), and 84% of the remaining *Plateau* forests are found in the Pontal do Paranapanema Region, in the westernmost extremity of São Paulo State (Valladares-Padua *et al.* 2002). In 1941, while still entirely forested, the entire western part of São Paulo, comprising an area of ~2,600 km^2, was decreed a forest reserve, the "*Grande Reserva do Pontal*" (Great Reserve of the Pontal) (Valladares-Padua 1993; Leite 1998). Since then, the history of the Pontal do Paranapanema Region has been marked by a series of conflicts over land ownership and a complex process of Agrarian Reform, which has led to the almost complete destruction and fragmentation of its forests. Deforestation in the region from 1987 to 2001 occurred at a rate of 1.5% year^{-1} (Cullen 2007).

Only 17% of the Pontal do Paranapanema Region remains covered with forests (Uezu *et al.* 2008). The remaining forests includes: Morro do Diabo State Park, which protects 370 km^2 of forest; Black-Lion-Tamarin Ecological Station, a federal protected area created in 2002 encompassing the four largest forest fragments located around Morro do Diabo and comprising an additional 67 km^2 of protected habitat; and a multitude of small forest fragments from 0.02-20 km^2 scattered throughout the region, comprising a further 60 km^2 of forest (Ditt 2002; Uezu *et al.* 2008). Most of the small forest fragments lie within private properties, while some are located in Agrarian Reform settlements and so are owned by the State. The landscape matrix is mainly composed of pasture land for cattle ranching (60%) and agricultural crops (15%) (Uezu *et al.* 2008).

In contrast to the eastern part of the Atlantic Forest biome, the process of deforestation of the Atlantic Forest of the Interior in the Pontal do Paranapanema Region is relatively recent, approximately 60 years. Therefore, while there has been an extensive loss of habitat, most of the forest remnants of the Pontal do Paranapanema Region still support an outstanding diversity of species of flora and fauna of the Atlantic Forest of the Interior, many of them endemic and/or threatened with extinction. Some of the larger forest fragments in the region, particularly Morro do Diabo State Park, still support populations of several species of large mammals, including lowland tapirs. During a biodiversity assessment carried out in the Pontal do Paranapanema Region, all forest fragments larger than 4 km^2 were surveyed for flora and fauna (Ditt 2002). The presence of tapirs was confirmed in eight of these forest fragments, including Morro do Diabo and seven smaller forest fragments in its surroundings. Tapirs were absent in six forest fragments surveyed during the study, characterising local extinctions most probably due to overhunting (Cullen 1997; Cullen *et al.* 2000). Nevertheless, although tapirs have been affected by the past processes of habitat fragmentation, they still survive in some of these forests.

Additionally, tapirs have the ability to cross areas of low quality habitat, such as agricultural crops and pasture lands, and move through the landscape matrix in between forest fragments (Flesher 2007). During this study, I gathered a considerable amount of data on tapir movements throughout the fragmented landscape of the Pontal do Paranapanema Region. Tapirs moved between Morro do Diabo and the surrounding small forest fragments, as well as amongst the small forest fragments themselves, thus characterising a certain level of metapopulation dynamics. These landscape movements were observed across rather short-scales when compared to the long distance movements observed for large cats such as jaguars, pumas and ocelots also in the Pontal do Paranapanema Region (Cullen 2007). Nevertheless, data from this study indicates that given the proper conditions in terms of habitat quality and resources and in the absence of threats, tapirs have the capability to recolonise forest fragments and maintain a certain level of genetic flow between different populations. In genetic terms, the short period since fragmentation occurred in the landscape of the Pontal do Paranapanema Region (from 5-6 tapir generations) probably means that patterns of genetic structure are still in transition, and therefore genetic drift and inbreeding have not been observed yet (Gonçalves da Silva 2007). Thus, the Atlantic Forest of the Interior of the Pontal do Paranapanema Region is the perfect environment for the assessment of the long-term persistence and viability of animal populations across fragmented landscapes.

1.2 Thesis Aims and Structure

In this thesis, I used data from a 12-year study on lowland tapirs in the Atlantic Forests of the Interior of the Pontal do Paranapanema Region, São Paulo State, Brazil, to substantiate an assessment of the long-term persistence and viability of tapir populations across a severely fragmented landscape. The main goal of this thesis was to understand what lowland tapirs require in terms of space, habitat and population abundance in order to remain demographically and genetically healthy, persist and be viable across the fragmented landscape of the Atlantic Forest of the Interior.

This goal was achieved through two different approaches:

- Empirical assessment of the persistence and viability of tapir populations based on ecological characteristics of the species including: (i) spatial ecology, (ii) intra-specific interactions, (iii) spatial and temporal interactions between tapirs and the landscape, and (iv) population sizes. The different aspects of the empirical assessment were explored in Chapters 3, 4, and 5.

- Modelling of tapir population viability through the use of a computer simulation model of Population Viability Analysis (PVA). The modelling approach was explored in Chapter 6.

Chapter 1 has already introduced the main questions posed by this thesis and explained why lowland tapirs and the Atlantic Forest of the Interior in the Pontal do Paranapanema, São Paulo, Brazil, are appropriate models to illustrate an assessment of the viability of animal populations across severely fragmented landscapes.

Chapter 2 provides detailed information about the study species and the study area. The first part of the chapter describes lowland tapirs, providing information about taxonomy and evolution, morphology, geographic distribution, ecology and behaviour, and lastly the conservation status of the species and the threats it faces in the wild. The second part of the chapter is dedicated to a comprehensive overview of the history of destruction and fragmentation of the Atlantic Forest biome and its current conservation status, providing specific details about the Atlantic Forest of the Interior and the Pontal do Paranapanema Region. This includes a description of Morro do Diabo State Park where most of the tapir data were collected during this study. The third and final part of the chapter provides general information about the study including details about logistics and personnel, different field methods used for data collection, timeframe of study, as well as required research permits.

Chapter 3 is dedicated to analysing tapir spatial ecology and intra-specific interactions. The purpose of this chapter was to determine tapir spatial requirements and how these influence the long-term survival and persistence of tapir populations in the Atlantic Forest. Analysis of tapir home range size, structure, and seasonality in Morro do Diabo, as well as the description of tapir movements through the fragmented landscape of the Pontal do Paranapanema Region, were used to determine tapir spatial ecology. Estimates of home range overlap and overlap of core areas of use were used to examine aspects of territoriality and intra-specific interactions. A large part of this chapter was dedicated to providing an overview of the use and reliability of radio-telemetry for studying tapirs over the long-term. I presented detailed information about the different phases involved in the process of using radio-telemetry including methods of capture, immobilisation protocols and manipulation procedures, as well as data collection and sampling design. An additional analysis included in this chapter involved the determination of the minimum amount of time and minimum number of locations required to determine tapir home range size, a critical piece of information for the design of future tapir studies.

Chapter 4 is dedicated to determining the abundance of tapir populations in Morro do Diabo State Park and surrounding Atlantic Forest fragments in the Pontal do Paranapanema Region. Population size is a fundamental demographic element and a cornerstone of ecology, which has widespread implications for population structure and dynamics, as well as for determining the viability of animal populations over the long-term. Yet, making accurate estimates of population size is very difficult. Animals are often difficult to capture or observe, and the associated costs and effort of making absolute counts or censuses are prohibitive. Consequently, animal ecologists have to rely on indirect methods to estimate population abundance and then derive or estimate population size. I estimated the density of the tapir population in Morro do Diabo through the use of three different methodologies including radio-telemetry, nocturnal line-transect sampling, and Footprint Identification Technique (FIT). Various methods of data analysis were applied and I obtained 10 different estimates of tapir density for Morro do Diabo. I then selected the most appropriate density estimate to derive tapir population sizes in Morro do Diabo and surrounding forest fragments where the presence of tapirs had been previously confirmed. Additionally, part of this chapter was dedicated to comparing the three density estimators according to a selected set of criteria including cost, requirement of personnel, and field effort. Another criterion was the invasiveness of the method. The growing need to census and monitor wildlife populations over time makes the development, evaluation, and validation of suitable techniques for estimating abundance a priority. The advantages and disadvantages of each method applied during this study, as well as their accuracy and reliability for long-term tapir monitoring were presented and discussed.

Chapter 5 explores the spatial and temporal interactions between tapirs and the fragmented landscape of the Pontal do Paranapanema Region. I first looked at the extent of occurrence of different habitat types within tapir home ranges and core areas of use in Morro do Diabo. This allowed me to gain knowledge into how tapirs establish and structure their home ranges, and what kinds of habitats they incorporate within their main areas of use. Second, I examined how tapirs actually use these different habitat types. I determined the availability and use of different habitat types within tapir home ranges, and examined which habitats were significantly selected or avoided by them. The examination of habitat selection provided evidence of whether tapir use of different habitat types occurred in proportion to their availability in the study site. Lastly, I analysed tapir activity patterns in Morro do Diabo. I determined the main peaks of activity, as well as patterns of habitat use in relation to activity. These analyses provided information about what types of habitat tapirs use for their main activities including foraging, travelling, and resting. All this information was then used to determine how the spatial and temporal interactions between tapirs and the mosaic of different habitats found within the landscape of the Pontal do Paranapanema Region relate to the survival and long-term persistence of tapir populations in the Atlantic Forest.

Chapter 6 focuses on modelling the viability of tapir populations through the use of Population Viability Analysis (PVA). I developed a robust VORTEX baseline model reflecting the biological potential of tapirs in Morro do Diabo, and carried out sensitivity analysis to evaluate the effect of selected reproductive and mortality parameters on the stochastic growth rate of lowland tapir populations. Next, I carried out an analysis of the Minimum Viable Population (MVP) for tapirs in Morro do Diabo. I then used the baseline model to evaluate the impact of fire, road-kill and infectious diseases, analysing how these factors affect the probability of long-term persistence of tapirs in Morro do Diabo. Lastly, I created a metapopulation scenario including Morro do Diabo and surrounding forest fragments and analysed the probability of extinction of the different populations and of the metapopulation as a whole. As an example of conservation strategy, I modelled the establishment of corridors between Morro do Diabo and surrounding forest fragments, and analysed the impact these corridors would have on the long-term viability of the lowland tapir populations in the Pontal do Paranapanema Region.

Chapter 7 concludes this thesis by using information about tapir ecological requirements and results from population modelling to substantiate the design of conservation strategies to promote the long-term survival and persistence of tapir populations in severely fragmented landscapes. In addition, this chapter provides recommendations on what further data are needed to allow for the assessment of viability of tapir populations over the long-term. Lastly, I conclude with a general discussion about the factors that are determinant for the long-term persistence and viability of animal populations across fragmented landscapes.

Chapter 2

Study Species, Study Area and General Methods

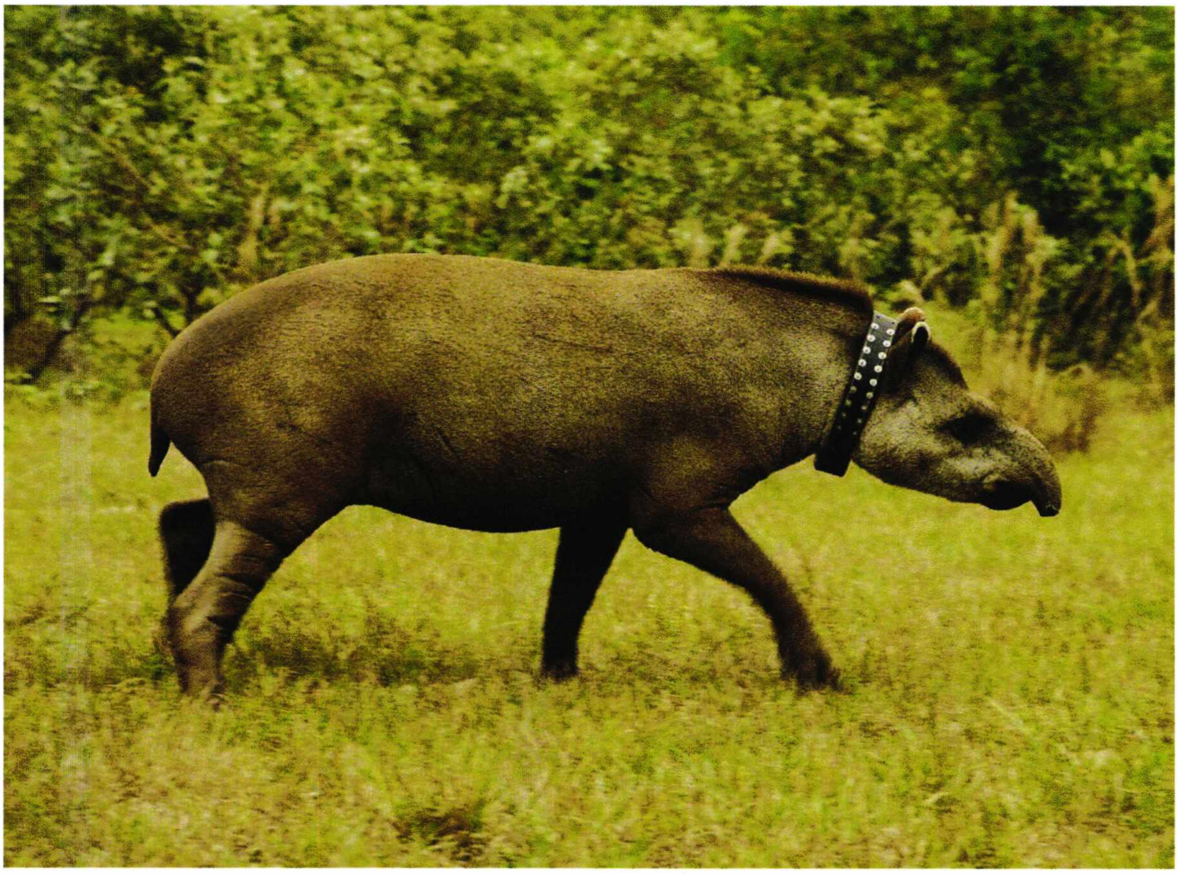


Photo by Patrícia Medici

2.1 Introduction

This chapter provides detailed information about the study species and the study area, as well as general methods used in this long-term research study. The first part of the chapter consists of a detailed description of lowland tapirs, providing information on aspects of taxonomy and evolution, morphology, geographic distribution, ecology and behaviour, as well as the conservation status of the species and the threats it faces in the wild. The second part provides an overview of the history of destruction and fragmentation of the Atlantic Forest biome and its current conservation status, especially in Brazil, including specific details about the Atlantic Forest of the Interior and the Pontal do Paranapanema Region. This includes a description of Morro do Diabo State Park, the protected area where most of the tapir data were collected during this study. The third and final part of the chapter provides general information about the study including details of logistics and personnel, required permits, field methodologies used for data collection, and timeframe of study.

2.2 The Lowland Tapir

2.2.1 Taxonomy and Evolution

The lowland tapir, *Tapirus terrestris*, also known as Brazilian or South American tapir, is an ungulate of the order Perissodactyla. The lowland tapir is one of the four surviving species of a taxon that has been very successful in the past (Eisenberg 1997). The other three species are the Baird's tapir (*Tapirus bairdii*) in Central and northern South America, the mountain tapir *Tapirus pinchaque*), in the Andes of South America, and the Malayan tapir (*Tapirus indicus*) in Southeast Asia. According to Eisenberg (1997), the family Tapiridae was first recognisable as a taxonomic entity in the Eocene of North America, nearly 50 Million years ago. The genus *Tapirus* first appeared in the Miocene (25-5 Million years ago), so extant tapirs derive from an ancient lineage that is related to the primitive horse and to the rhinoceros. Prehistoric tapirs inhabited Europe, North America and Southeast Asia, including China. No remains have been found on the continents of Africa or Australia. Given the intermittent connections between North America and Asia via the Bering Strait, tapirs soon appeared in Euro-Asia. With the completion of the Isthmus of Panama between North and South America, during the Pliocene (7-2 Million years ago), tapirs entered South America (Eisenberg 1997).

2.2.2 Morphology

Many of the morphological characteristics of tapirs are primitive, including unreduced dental formula, short legs with retention of complete ulna and fibula, and retention of tetradactyl *manus* and tridactyl *pes*, all features seen in the first member of the Perissodactyla, the *Hyracotherium* (Janis 1984). The dental formula of adult tapirs is 2X (I-3/3, C-1/1, PM-4/3, M-3/3) giving a total of 42 teeth in both males and females. The upper third incisors are large and well developed, while the upper canines are reduced and separated from the incisors by a narrow diastema. The lower third incisors are reduced and the lower canine is well developed, occluding with the canine-like upper third incisors. There is a large diastema between canines and premolars in both jaws (Padilla & Dowler 1994).

Tapirs have a solid body structure, shaped round in the back and tapering in the front, well-suited for rapid movement through thick underbrush (Eisenberg 1997) (Figure 2.1). The colour of adult lowland tapirs is blackish brown dorsally with the ears edged in white; the chest, venter and limbs are dark brown; the cheeks are grizzled brown and gray (Padilla & Dowler 1994). A fibrous tissue layer lies beneath the epidermis of tapirs (Frädrich & Thenius 1972). The skin of lowland tapirs is thickest at the nape, and often covered by scars, scratches, and bruises (Hershkovitz 1954). Lowland tapirs have a well developed sagittal crest that runs from the base of the muzzle to the middle of the back (Padilla & Dowler 1994), which is derived from fat and soft tissues and covered by long black hair (Hershkovitz 1954). The sagittal crest is thought to help escape predators, which usually seize the dorsum of the neck (Medici 2001). Young of all four tapir species are dark with yellow or white stripes and spots, which serves as camouflage against predation (Figure 2.2). This pattern begins to fade at three months and is completely gone after 5-6 months of life, although some vestiges of spotting may remain in young adults (Hershkovitz 1954).

Tapirs have relatively long, laterally compressed skulls with a high braincase and convex profile. The nasal bones are short, arched and freely projecting. The nasal opening is very large. Tapirs have a short, fleshy proboscis derived from muscle and soft tissues from the snout and upper lip. The proboscis is highly mobile and sensitive to touch, and is important for food manipulation and ingestion (Padilla & Dowler 1994). Tapir eyes are small and flush with the side of the head; their ears are oval, erect, and not very mobile (Eisenberg 1997). Tapirs have poor eyesight but good hearing and olfactory senses (Frädrich & Thenius 1972).

The feet of tapirs are mesaxonic (Padilla & Dowler 1994). The forefoot has four main digits, and a smaller one (the fifth) is only used when the tapir is walking on soft ground. The hind feet have three digits. All the toes are hoofed. The splayed feet, help tapirs walk in muddy and soft ground. The weight of the body is divided between an elastic cushion under the feet and the central digits, which becomes evident in the tapir footprints.

The lowland tapir is the second largest terrestrial mammal in South America, the first being the Baird's tapir (*Tapirus bairdii*). According to Padilla & Dowler (1994), adult lowland tapirs weigh from 150-250 kg. In captivity, adult female lowland tapirs were usually observed to be 25-100 kg heavier than males (Barongi 1986; Barongi 1993). According to data collected from captured lowland tapirs during this study in Morro do Diabo, average tapir weights were 233 kg for adult females, 208 kg for adult males, 200 kg for sub-adult females, and 195 kg for sub-adult males (Table 2.1). There was no difference in weight when comparing between the sexes for both adults (T=94.000; N=10-14; P=0.074) and sub-adults (t=-0.156; DF=4; P=0.884). Two juveniles captured during the study (1 male and 1 female) weighed from 80-100 kg. Newborn tapirs usually weigh from 3-6 kg (Padilla & Dowler 1994). In captivity, lowland tapir calves gain an average of 2.5 kg per week and are completely weaned at 4 months of age (Barongi 1993). Growth is usually completed at 18 months of age (Young 1961).

Table 2.1. Mean weights (kg) of 33 lowland tapirs (19 females and 14 males, or 27 adults and 6 sub-adults) captured in Morro do Diabo State Park, São Paulo, Brazil. (N=number of tapirs; AV=average; SD=standard deviation; Min=minimum; Max=maximum).

Weight (kg)	**N**	**AV**	**SD**	**Min**	**Max**
ADULT FEMALES	17	**233**	38.3	200	300
ADULT MALES	10	**208**	37.6	180	280
SUB-ADULT FEMALES	2	**200**	14.1	180	200
SUB-ADULT MALES	4	**195**	42.0	150	250

Mallinson (1969) observed that female lowland tapirs in captivity seemed to be longer on average than males. Padilla & Dowler (1994) noted a total body length of 204 cm for adult male lowland tapirs, and 221 cm for females. Data collected during this study in Morro do Diabo showed that for the great majority of the corporal measurements obtained from captured tapirs, females presented higher averages than males, in both adult and sub-adult age classes (Tables 2.2 and 2.3). For six out of 13 measurements adult females were significantly larger than adult males (Table 2.2). No differences were observed between the sexes in sub-adults (Table 2.3). Table 2.4 provides corporal measurements of two juvenile tapirs captured during the study.

Table 2.2. Mean values of 13 corporal measurements (cm) obtained from 30 adult lowland tapirs (19 females and 11 males) captured in Morro do Diabo State Park, São Paulo, Brazil. (N=number of tapirs; AV=average; SD=standard deviation; Min=minimum; Max=maximum; *Indicates a significant difference between the sexes).

Corporal Measurements (cm)	**ADULT Females**					**ADULT Males**					**Significant Differences**
	N	**AV**	**SD**	**Min**	**Max**	**N**	**AV**	**SD**	**Min**	**Max**	
Neck circumference*	18	**86**	7.4	74	98	11	**79**	6.9	64	88	t=2.448; DF=27; **P=0.021**
Head length	18	**48**	4.8	40	55	9	**48**	5.2	39	55	t=-0.357; DF=25; P=0.724
Head width	15	**42**	9.9	29	70	10	**38**	4.6	31	44	t=1.223; DF=23; P=0.234
Full length (dorsum)*	19	**221**	9.8	208	242	11	**205**	11.7	191	223	t=3.992; DF=28; **P=<0.001**
Full length (lateral)*	16	**202**	12.3	174	223	9	**186**	23.4	130	216	T=79.500; N=9-16; **P=0.036**
Front leg length	18	**70**	9.0	51	81	8	**65**	9.7	53	79	t=1.376; DF=24; P=0.181
Rear leg length	17	**72**	8.3	58	83	8	**65**	6.9	52	75	t=2.058; DF=23; P=0.051
Thorax circumference*	17	**144**	12.8	118	168	10	**129**	7.8	120	146	t=3.224; DF=25; **P=0.004**
Abdomen circumference	14	**169**	19.0	132	198	4	**152**	9.1	142	164	t=1.615; DF=16; P=0.126
Front height*	17	**108**	8.4	83	118	10	**101**	9.7	83	113	T=94.500; N=10-17; **P=0.024**
Rear height*	18	**110**	8.5	90	120	10	**101**	7.0	89	109	T=89.000; N=10-18; **P=0.008**
Ear length	16	**13**	1.7	11	16	9	**13**	1.5	10	15	t=0.439; DF=23; P=0.665
Distance between eyes	15	**23**	3.6	15	28	9	**24**	2.5	20	28	t=-0.947; DF=22; P=0.354

Table 2.3. Mean values of 13 corporal measurements (cm) obtained from 6 sub-adult lowland tapirs (2 females and 4 males) captured in Morro do Diabo State Park, São Paulo, Brazil. (N=number of tapirs; AV=average; SD=standard deviation; Min=minimum; Max=maximum).

Corporal Measurements (cm)	**SUB-ADULT Females**					**SUB-ADULT Males**					**Significant Differences**
	N	**AV**	**SD**	**Min**	**Max**	**N**	**AV**	**SD**	**Min**	**Max**	
Neck circumference	4	**83**	6.2	76	91	2	**81**	2.1	80	83	t=0.264; DF=4; P=0.805
Head length	4	**46**	5.0	42	53	2	**47**	8.5	41	53	t=-0.191; DF=4; P=0.858
Head width	4	**36**	4.0	32	41	2	**32**	2.1	31	34	t=1.187; DF=4; P=0.301
Full length (dorsum)	4	**213**	5.2	207	219	2	**198**	9.2	192	205	t=2.611; DF=4; P=0.059
Full length (lateral)	2	**165**	10.6	158	173	1	**184**	12.4	184	184	N too small to perform test
Front leg length	3	**69**	7.1	61	75	2	**64**	7.8	59	70	t=0.623; DF=3; P=0.578
Rear leg length	3	**68**	6.8	60	73	2	**65**	2.8	63	67	t=0.504; DF=3; P=0.649
Thorax circumference	3	**140**	17.3	130	160	2	**118**	0.7	118	119	t=1.665; DF=3; P=0.195
Abdomen circumference	1	**144**	8.3	144	144	1	**142**	8.3	142	142	N too small to perform test
Front height	4	**103**	7.9	92	111	2	**97**	7.8	92	103	t=0.771; DF=4; P=0.484
Rear height	4	**108**	8.1	97	115	2	**102**	7.8	97	108	t=0.831; DF=4; P=0.453
Ear length	4	**16**	1.8	14	18	2	**13**	1.4	12	14	t=2.000; DF=4; P=0.116
Distance between eyes	3	**23**	4.2	20	28	2	**20**	1.4	19	21	t=1.044; DF=3; P=0.373

Table 2.4. Mean values of 13 corporal measurements (cm) obtained from 2 juvenile lowland tapirs (1 male and 1 female) captured in Morro do Diabo State Park, São Paulo, Brazil. (N=number of tapirs; AV=average; SD=standard deviation; Min=minimum; Max=maximum).

Corporal Measurements (cm)	**JUVENILES**				
	N	**AV**	**SD**	**Min**	**Max**
Neck circumference	2	**73**	9.9	66	80
Head length	2	**44**	2.1	43	46
Head width	2	**34**	1.4	33	35
Full length (dorsum)	2	**176**	5.7	172	180
Full length (side)	2	**158**	9.2	152	165
Front leg length	2	**66**	8.5	60	72
Rear leg length	2	**70**	5.7	66	74
Thorax circumference	2	**110**	5.7	106	114
Abdomen circumference	2	**132**	2.8	130	134
Rear height	2	**89**	2.1	88	91
Front height	2	**89**	0.0	89	89
Ear length	2	**13**	0.7	13	14
Distance between eyes	2	**14**	2.8	12	16

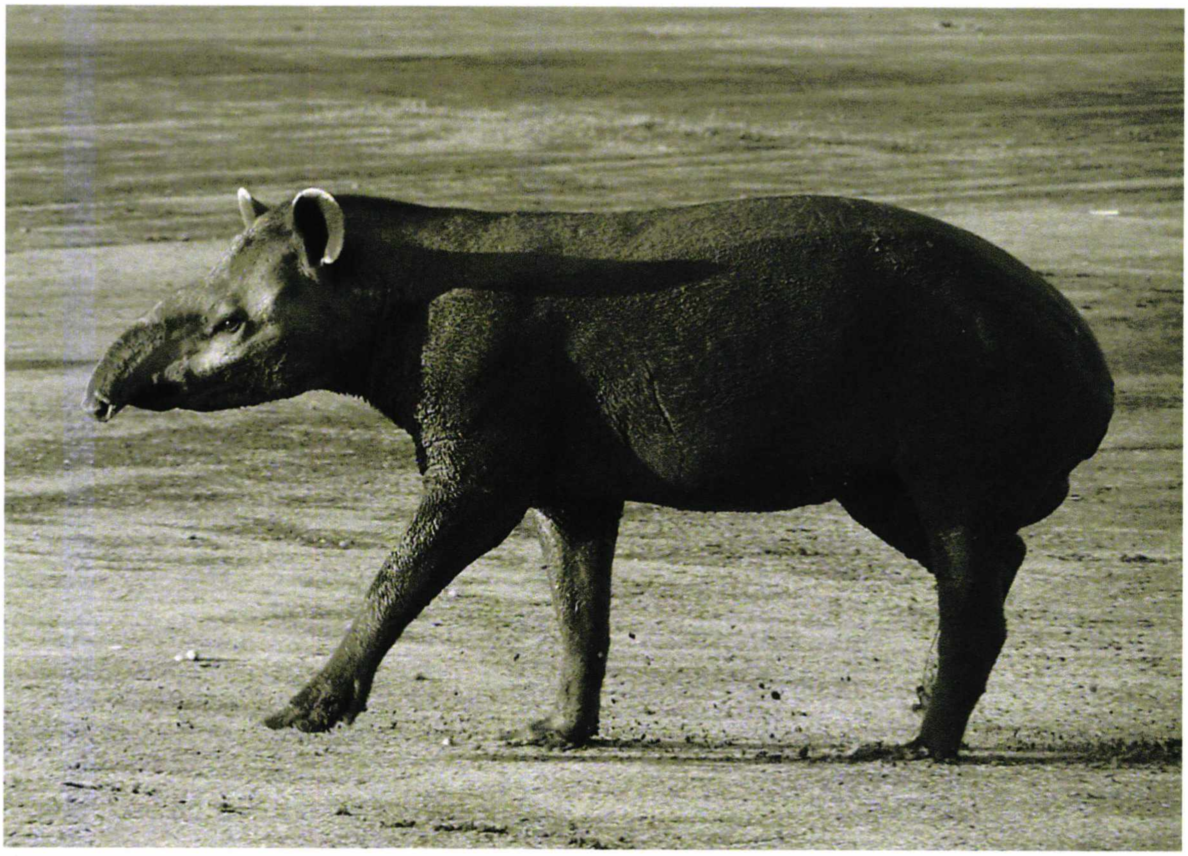


Figure 2.1. The lowland tapir (*Tapirus terrestris*), also known as South American or Brazilian tapir. Photo by Richard E. Bodmer.

Figure 2.2. Captive lowland tapir calf at approximately 30 days of age. Photo by Kelly Russo.

2.2.3 Geographic Distribution

The lowland tapir has the widest range of the four living species and which extends from north-central Colombia and east of the Andes throughout most of tropical South America down to north eastern Argentina and Paraguay, at elevations up to 2000 m (Hershkovitz 1954; Emmons & Feer 1997; Eisenberg 1997; Medici *et al.* 2007a). The species occurs in 11 different countries including Argentina, Bolivia, Brazil, Colombia, Ecuador, Guyana, French Guyana, Paraguay, Peru, Suriname and Venezuela. The historic distribution of this species covered ~13.1 million km^2 (Taber *et al.* 2008).

The Lowland Tapir Range-Wide Assessment carried out by the Wildlife Conservation Society (WCS) has identified the presence of lowland tapirs at 1,213 sites and the species was judged extinct in another 40 sites across its range (Taber *et al.* 2008). According to this assessment, the lowland tapir has become extinct across ~14% of its range, and its current distribution has declined to 11.2 million km^2. Range contractions have mostly occurred in north western South America, coastal Venezuela, northeast Brazil, and along the southern fringes of the species distribution in Argentina and Brazil. Approximately 41% of the historic range of the species was classified as being of low or medium probability for long-term survival, in which only small, isolated, and scattered populations will persist. However, populations were still broadly intact across 44% of its historic range. In Brazil specifically, the lowland tapir has disappeared from over 1 million km^2 or 12% of its country range. The species distribution range in Brazil still covers over 7 million km^2, but appears to have a high probability of long-term survival in only about a third of its historic range (Taber *et al.* 2008) (Figure 2.3).

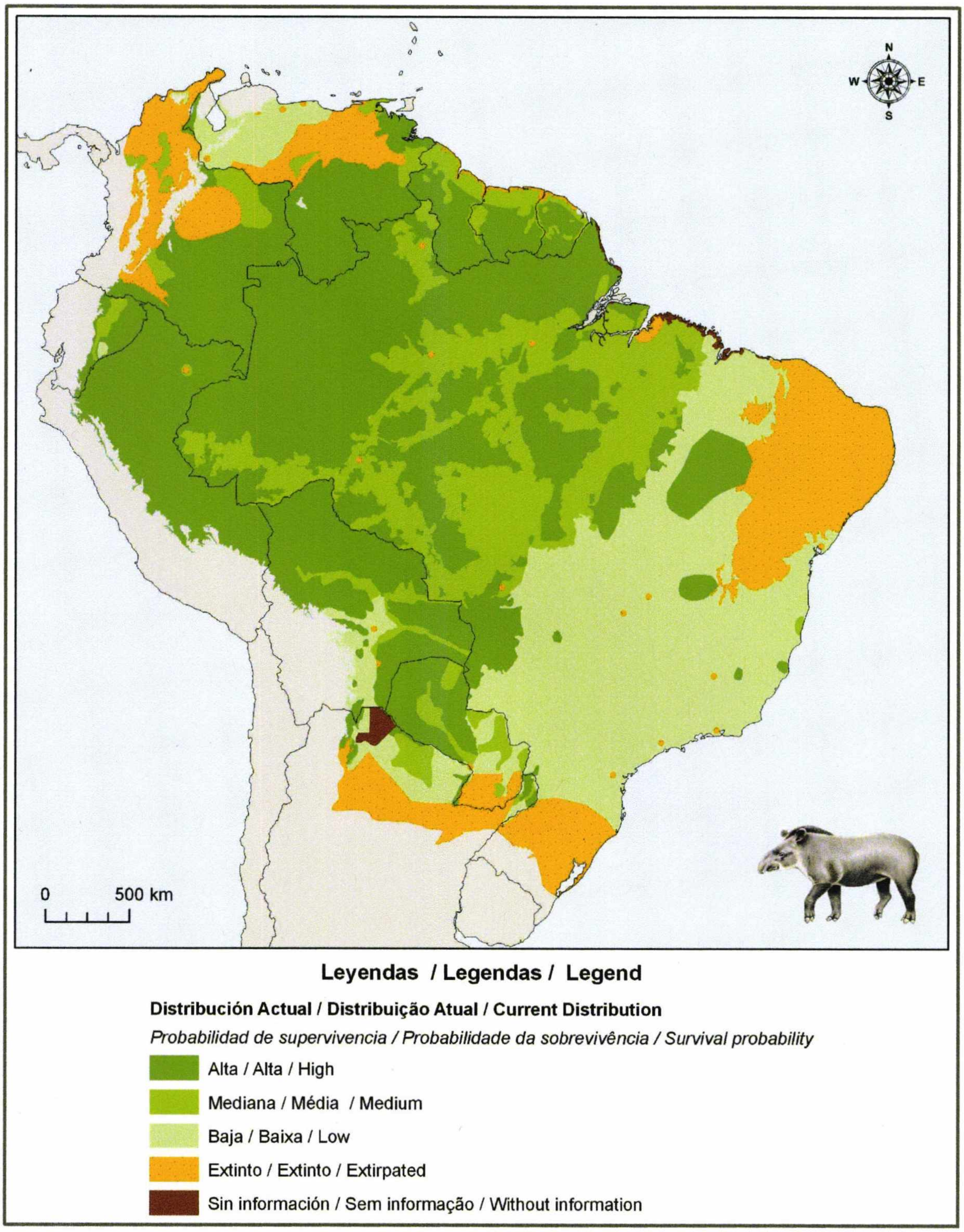


Figure 2.3. Map of current distribution and probability of survival of the lowland tapir. Extracted from the Lowland Tapir Range-Wide Assessment Report (Taber *et al.* 2008).

The Lowland Tapir Population and Habitat Viability Assessment (PHVA) Workshop (Medici *et al.* 2007a) was held by the IUCN/SSC Tapir Specialist Group (TSG) and the IUCN/SSC Conservation Breeding Specialist Group (CBSG), and identified 21 different biomes where lowland tapirs are still found throughout their range (Table 2.5), with the largest populations currently existing in the Amazon. Some of these biomes are specific of certain range countries. In Brazil, lowland tapirs are found in five biomes: Amazon, Atlantic Forest, Cerrado, Pantanal, and Araucaria Forests.

Table 2.5. List of 21 biomes where lowland tapirs occur. Extracted from the Lowland Tapir Population and Habitat Viability Assessment (PHVA) Workshop Final Report (Medici *et al.* 2007a).

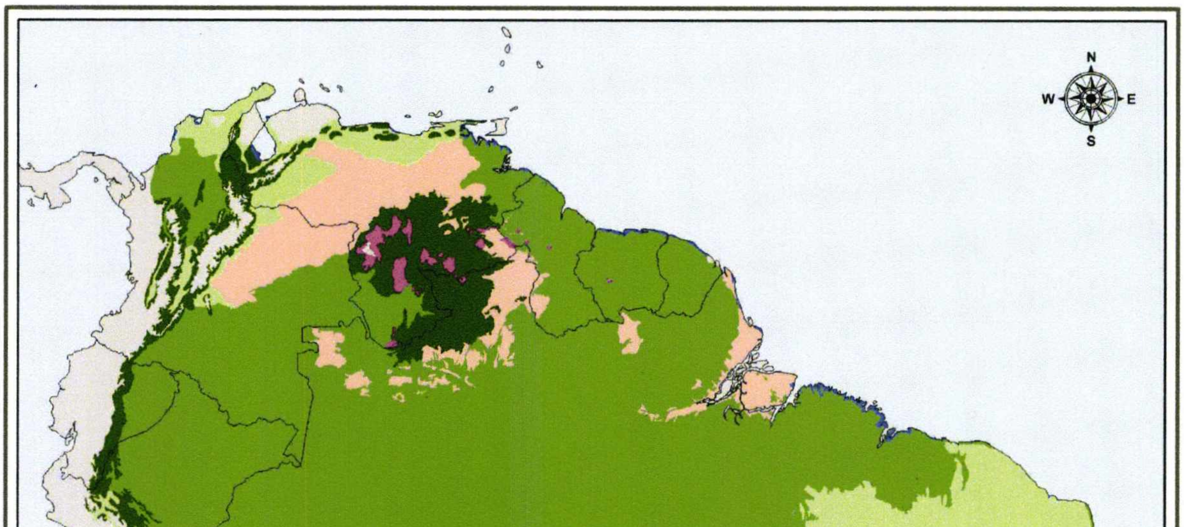
General Biomes
North Eastern Amazon
South Eastern Amazon
Upper Amazon
Amazonian Savannas
Dry Chaco
Humid Chaco
Subtropical Andean Forests
Llanos
Atlantic Forest of the Interior
Pantanal
Yunga Forests
Brazilian Biomes
Araucária Forests
Cerrado
Coastal Atlantic Forest
Colombian Biomes
Oriental Amazon
Occidental Amazon
Orinoquía
Northeast Antioqueño
Sierra Nevada de Santa Marta
Suriname Biomes
Coastal Forests
Venezuelan Biomes
Northern Andes

2.2.4 Ecology and Behaviour

2.2.4.1 Habitat Requirements

As its name indicates, the lowland tapir commonly inhabits tropical lowland South American rainforests but can also be found in a wide range of other habitat types including tropical moist forests, xeric Chaco and Cerrado forest, savannah wetlands and lower montane forests (Eisenberg 1997). The Lowland Tapir Range-Wide Assessment (Taber *et al.* 2008) identified six main categories of habitat where lowland tapirs occur comprising: (i) tropical and sub-tropical moist broadleaf forests; (ii) tropical and sub-tropical moist to seasonally moist montane forests; (iii) tropical and sub-tropical dry forests, savannahs and shrub lands; (iv) tropical and sub-tropical seasonally moist grasslands and savannahs; (v) montane grasslands; and, (vi) mangroves (Figure 2.4). Therefore, the lowland tapir appears to be adapted to a diverse array of environments found throughout its distribution range. Nevertheless, a number of studies have identified patterns of habitat preference and selection in tapir species (Bodmer 1990b; Fragoso 1991a; Fragoso 1991b; Naranjo 1995; Foerster 1998; Naranjo & Cruz-Aldán 1998; Muench 2001; Foerster & Vaughan 2002; Ayala 2003; Lizcano 2006; Tobler *et al.* 2006; Tobler 2008).

Palm forests are thought to be important tapir habitat (Brooks *et al.* 1997; Fragoso 1997; Olmos *et al.* 1999; Tófoli 2006). In the north eastern region of the Brazilian Pantanal, tapirs show high preference for Acuri palm forests (*Scheelea phalerata*) when compared to other vegetation types. Accordingly, potential tapir distribution models demonstrate high occurrence probabilities in such habitat areas (Cordeiro 2004). In addition, tapirs are generally closely associated with riparian forests, marshes, lakes and streams (Padilla & Dowler 1994; Medici 2001). Tapirs defecate in water or in dry seasonal streams and ponds (Eisenberg 1989; Bodmer 1991a). However, exceptions to this behaviour have been observed in other areas where tapir faeces were found in dry areas or near forest edges (Affonso 1998; Galetti *et al.* 2001; Tófoli 2006). Some studies have found that tapirs may use seasonal latrines including numerous faecal piles all together in the same location (Galetti *et al.* 2001; Tófoli 2006).



Leyendas / Legendas / Legend

Tipos Principales de Hábitat / Habitats Principais / Major Habitat Types

🟩 Bosques lluviosos latifoliados tropicales y subtropicales / Florestas Úmidas Latifoliadas Tropicais e Subtropicais / Tropical & subtropical moist broadleaf forests

■ Bosques lluviosos montanos a estacionalmente lluviosos tropicales y subtropicales / Florestas Montanas Úmidas e Estacionalmente Úmidas Tropicais e Subtropicais / Tropical & subtropical moist to seasonally moist montane forest

▨ Bosques secos, sabanas y arbustales tropicales y subtropicales / Florestas secas tropicais e subtropicais, Savanas e vegetação arbustiva / Tropical & Subtropical dry forests, savannas & shrublands

🟧 Pastizales y sabanas estacionalmente lluviosos tropicales y subtropicales / Campos e Savanas tropicais e subtropicais estacionalmente Úmidos / Tropical & Subtropical seasonally moist grasslands & savannas

🟪 Pastizales montanos / Campos Montanos / Montane grasslands

🟦 Manglares / Manguezais / Mangroves

Figure 2.4. Map of main categories of habitat where lowland tapirs occur. Extracted from the Lowland Tapir Range-Wide Assessment Report (Taber *et al.* 2008).

2.2.4.2 Feeding Behaviour

Tapirs shelter themselves in forests and thickets during the day and emerge at night to feed in bordering grassy or scrubland areas, marshes, lakes and streams (Padilla & Dowler 1994; Medici 2001). These daily movements result in well-worn paths (Husson 1978). Tapirs spend up to 90% of their active hours on foraging. They consume multiple small meals throughout their active periods, a behaviour that is, in part, a function of their limited stomach capacity when compared to the ruminant stomach. As a hindgut fermenter, the tapir gastrointestinal tract is very similar to that of the horse. When foraging, tapirs usually do not follow a regular path, but prefer to push their way through the jungle. The extensible proboscis is used to strip leaves and pluck fruits. Fruit may be taken from low shrubs or as fallen fruit on the ground. Tapirs will occasionally stand on their hind feet and reach with their prehensile proboscis nearly three metres from the ground in order to obtain food (Medici 2001).

Tapirs are exclusively herbivorous. They have a broad diet composition, feeding on a wide array of plant species and many different plant parts including the leaves, buds, twigs, bark, flowers and fruits of low-growing, terrestrial plants and they also consume aquatic vegetation occasionally (Terwilliger 1978; Janzen 1982; Williams 1984; Bodmer 1991a; Naranjo 1995; Salas & Fuller 1996; Tobler 2002; Tófoli 2006; Tobler 2008). In the Bolivian Chaco, lowland tapirs have successfully adapted to seasonal droughts, and to diets that include a large proportion of cactus fibre (Soto 2002). Over 170 species of fruit in over 60 different families have so far been identified as being eaten by the lowland tapir throughout its range (Bodmer 1991a; Rodrigues *et al.* 1993; Salas & Fuller 1996; Olmos 1997; Herrera *et al.* 1999; Fragoso & Huffman 2000; Henry *et al.* 2000; Galetti *et al.* 2001; Tófoli 2006; Tobler 2008). A study in a lowland rainforest of the Tabaro River Valley, Venezuela, showed that tapirs selectively browsed on 88 out of a total of at least 256 plant species and consumed fruit of 33 species (Salas & Fuller 1996). Tobler (2008) collected 135 lowland faecal samples in Los Amigos Conservation Concession in the Peruvian Amazon and found a total of 122 species of seeds, representing 68 genera and 33 families. In the semi-deciduous Atlantic Forest in Brazil, a study based on the analysis of 170 faecal samples and two stomach contents collected in Morro do Diabo State Park and surrounding forest fragments showed that lowland tapirs consumed 58 species of fruit from 23 different plant families (Tófoli 2006).

While tapirs are essentially browsers, they consume fruit extensively when available (Bodmer 1990a; Bodmer 1991a; Salas & Fuller 1996; Fragoso 1997; Fragoso & Huffman 2000; Henry *et al.* 2000; Foerster & Vaughan 2002; Tófoli 2006; Tobler 2008). Different studies in various parts of the geographic distribution of lowland tapirs have found different diet compositions. Tófoli (2006) showed that the diet of lowland tapirs in the Atlantic Forests of Morro do Diabo State Park consisted of 37% of fruit/seed and 63% of leaf/fibre. Bodmer (1990a) analysed stomach, cecal, and faecal samples of lowland tapirs in the Peruvian Amazon and reported that the species consumed 33% of fruit and 66% of leaf/fibre. A study carried out by Henry *et al.* (2000) in the tropical rainforests of French Guiana analysed the contents of 27 lowland tapir stomachs collected from local hunters; fruit comprised 24%, leaf 22%, and fibre 53%. In Noel Kempff Mercado National Park, Bolivia, 59 lowland tapir faecal samples were made up of 17% fruit, 62% leaf, and 21% fibre (Herrera *et al.* 1999). Affonso (1998) found that the diet of lowland tapirs at the Turvo State Park in Rio Grande do Sul, Brazil, consisted of ~56% of fruit. It has been suggested that tapirs consume fibrous vegetation for protein and depend on more digestible foliage and fruit for energy (Foose 1982). Depending on the availability of different food items, tapirs can shift their foraging strategy among habitat types and seasons.

Several studies have shown that palm fruits are important food resources for lowland tapirs (Bodmer 1991a; Fragoso 1997; Fragoso & Huffman 2000; Galetti *et al.* 2001; Tófoli 2006; Tobler 2008). Bodmer (1990a) found *Mauritia flexuosa* to be the single most important food item (76%) in the diet of tapirs in the Peruvian Amazon. The distribution of these palm patches appears to strongly influence the movement patterns of tapirs in the area. In a semi-deciduous fragment of Atlantic Forest in São Paulo State, Brazil, Galetti *et al.* (2001) found seeds of *Syagrus romanzoffiana* in 54% of 46 faecal samples collected over a period of four years. In Morro do Diabo, Tófoli (2006) showed that *Syagrus romanzoffiana* was the most frequently found fruit (18%) in lowland tapir faecal samples. *Syagrus romanzoffiana* is the most abundant and widespread palm species in the semi-deciduous Atlantic Forest (Galetti *et al.* 2001). These palms are abundant in Morro do Diabo and produce many fruits throughout the year (Faria & Pires 2006). This palm fruit is rich in carbohydrates and is widely consumed by a great diversity of birds and mammals, particularly during the dry season when other species of fruit are less available (Keuroghlian 1990).

Although the diet of lowland tapirs has been studied in several tropical locations in different countries including Brazil (Fragoso 1997; Olmos 1997; Fragoso *et al.* 2000; Galetti *et al.* 2001; Tófoli 2006), Colombia (Peña *et al.* 1996), French Guiana (Henry *et al.* 2000), Peru (Bodmer 1990a; Tobler 2008), and Venezuela (Salas & Fuller 1996), very little is known about the nutritional contents of food items consumed by tapirs in the wild. Lopes *et al.* (1980) provides results on fat, carbohydrate and protein content of several Amazonian fruits consumed by tapirs.

2.2.4.3 Spatial Requirements

The spatial requirements of tapirs are thought to vary with the carrying capacity of different habitats (Eisenberg 1997; Medici *et al.* 2007a). Lowland tapirs monitored by radio-telemetry in Kaa-Iya del Gran Chaco National Park, Bolivia, had a home range of 2.8 km^2 for males and 2.2 km^2 for females (Ayala 2003). Subsequent telemetry studies in Kaa-Iya National Park found an average tapir home range size of 2.5 km^2 (Noss *et al.* 2003) with little seasonal variation in size and some overlap between different individuals. The sizes of home ranges of lowland tapirs radio-tracked through GPS telemetry in Los Amigos Conservation Concession in the Peruvian Amazon varied from 1.1-3.9 km^2, with an average of 2.6 km^2 (Tobler 2008). Table 2.6 presents further estimates of lowland tapir home range size in different study areas.

2.2.4.4 Population Density

Lowland tapir population density tends to be low with estimates ranging from a high of 1.6 tapirs km^{-2} reported in Neotropical forests in undisturbed, non-hunted, or lightly hunted sites (Robinson & Redford 1986; Robinson & Redford 1991) to less than 0.3 tapirs km^{-2} (Cullen *et al.* 2000; Aquino *et al.* 2001; Aquino & Calle 2003; Haugaasen & Peres 2005; Desbiez 2007) in different regions and habitat types. In Amazonian forests, lowland tapirs are usually found in densities of 0.5 tapirs km^{-2} (Janson & Emmons 1990). Mendes-Pontes (2004) found exceptionally high densities of lowland tapirs (3.3-3.7 tapirs km^{-2}) in the Amazonian dry forests of Roraima, Brazil. In the Brazilian Pantanal, Schaller (1983) reports a density of 0.64 tapirs km^{-2}, while Desbiez (2007) found an average density of 0.21 tapirs km^{-2} (0.40 tapirs km^{-2} in forest habitat, and 0.13 tapirs km^{-2} in open grasslands habitat). For the semi-deciduous Atlantic Forest, lowland tapir densities estimated by Cullen *et al.* (2000) for three different forest fragments of different sizes and levels of conservation ranged from 0.30-0.47 tapirs km^{-2}. Table 2.7 presents all estimates of lowland tapir population density found in the available literature.

Table 2.6. Estimates of lowland tapir home range size (km^2) and other ranging behaviour parameters (home range overlap, core areas of use) obtained for different study areas and biomes in Brazil, Bolivia, and Peru.

Location	Biome	Country	Method	Home Range Size (km^2)	Reference
Brasília National Park Distrito Federal	Cerrado	Brazil	VHF radio-telemetry (1 month; 20 locations)	-- 1 male -- MCP 100%: **39.14 km^2**	Tarcísio Santos Jr. (unpublished results)
Lago Caiman - Noel Kempff Mercado National Park	Southern Amazon	Bolivia	VHF radio-telemetry (12 months; 10 locations)	-- 1 female -- MCP 95%: **16.4 km^2** Ellipse 95%: **48.78 km^2** Core Area = **≤ 4 km^2**	Herrera *et al.* (1999)
Kaa-Iya del Gran Chaco National Park	Chaco	Bolivia	VHF radio-telemetry (12 months; 2100 locations)	-- 5 tapirs - 2 females & 3 males -- MCP 95% - Males: **2.81 km^2** MCP 95% - Females: **2.18 km^2** Home range overlap: **25-75%**	Ayala (2003)
Kaa-Iya del Gran Chaco National Park	Chaco	Bolivia	camera-trapping	**0.97-3.74 km^2** (4 individuals 1st survey) **1.03-4.83 km^2** (4 individuals 2nd survey) **0.50-5.78 km^2** (6 individuals 3rd survey)	Noss *et al.* (2003)
Kaa-Iya del Gran Chaco National Park	Chaco	Bolivia	VHF radio-telemetry (22-29 months; 645-955 locations)	-- 5 tapirs - 2 females & 3 males -- MCP 95%: **2.48 km^2** Home range overlap: **32-55%** (average **43.5%**)	Noss *et al.* (2003)
Los Amigos Conservation Concession	Amazon	Peru	GPS radio-telemetry (7-182 days; 78-6185 locations)	-- 6 tapirs - 4 females & 2 males -- Kernel 95%: **1.06-3.86 km^2** Average: **2.61 km^2** Core Area 50% = **0.14-0.88 km^2** Core Area 25% = **0.05-0.33 km^2** Females: **2.86 km^2** Males: **2.11 km^2** MCP 95%: **0.95-3.53 km^2** Average: **2.25 km^2** Females: **2.53 km^2** Males: **1.66 km^2**	Tobler (2008)

Table 2.7. Estimates of lowland tapir population density (tapirs km^{-2}) obtained for different study areas and biomes across the species distribution range. Field method used and bibliographical reference are shown for each estimate.

Location	**Biome**	**Country**	**Method**	**Density Estimate** (tapirs km^{-2})	**Reference**
Morro do Diabo State Park São Paulo State	Semi-Deciduous Atlantic Forest	Brazil	line transect (diurnal)	0.20-**0.41**-0.84	Cullen *et al.* (2000)
Caetetús Ecological Station São Paulo State	Semi-Deciduous Atlantic Forest	Brazil	line transect (diurnal)	**0.47**	Cullen *et al.* (2000)
Mosquito Farm São Paulo State	Semi-Deciduous Atlantic Forest	Brazil	line transect (diurnal)	**0.30**	Cullen *et al.* (2000)
Mata dos Godoy State Park Paraná State	Semi-Deciduous Atlantic Forest	Brazil	direct count/area	**2.20-2.50**	Rocha (2001)
Brazilian Amazon	Amazon	Brazil	line transect (diurnal)	**0.11-0.52**	Peres (2000)
Kayapó Centre for Ecological Studies Pará State	Amazon	Brazil	line transect (diurnal)	**0.62**	Zimmerman *et al.* (2001)
Lago Uauaçú Central Western Amazonia	Amazon	Brazil	line transect (diurnal)	**0.23** (terra firme)	Haugaasen & Peres (2005)
Cocha Cachu Biological Station Manu National Park	Amazon	Peru	line transect (diurnal/nocturnal)	**0.5**	Janson & Emmons (1990)
Cocha Cachu Biological Station Manu National Park	Amazon	Peru		**< 0.5**	Terborgh (1992)
Manu National Park	Amazon	Peru		**5.0**	Ojasti (1993)
Reserva Comunal Tamshiyacu-Tahuayo	Amazon	Peru	line transect (diurnal)	**0.40** (persistently hunted site)	Bodmer *et al.* (1994)
Reserva Yavari Miri	Amazon	Peru	line transect (diurnal)	**0.60** (slightly hunted site)	Bodmer *et al.* (1994)
Reserva Nacional Pacaya Samiria	Amazon	Peru	line transect (diurnal)	**0.20**	Aquino & Calle (2003)
Reserva Nacional Pacaya Samiria	Amazon	Peru		**0.06-0.08**	Aquino *et al.* (2001)
Reserva Yavari Miri	Amazon	Peru		**0.31**	Salovaara *et al.* (2003)

Maracá Ecological Station Roraima State	Dry Forest Amazon	Brazil	line transect (diurnal/nocturnal)	**3.3-3.7** terra firme 4.1 (wet) / 2.5 (dry) mixed forest 3.7 (wet) / 3.7 (dry)	Mendes-Pontes (2004)
Acurizal Ranch Paraguay River Sub-Region	Pantanal	Brazil	direct count/area	**0.64**	Schaller (1983)
SESC Pantanal Barão de Melgaço Sub-Region	Pantanal	Brazil	line transect (diurnal) 23 sightings	Average **0.55** forest - 0.71 grasslands - 0.37	Cordeiro (2004)
Nhumirim Farm Nhecolândia Sub-Region	Pantanal	Brazil	line transect (diurnal) 16 sightings	Average **0.21** forest - 0.40 cerrado - 0.13	Desbiez (2007) Desbiez (2009)
SESC Pantanal Barão de Melgaço Sub-Region	Pantanal	Brazil	line transect (diurnal)	0.30-**0.55**-1.01	Trolle *et al.* (2007)
SESC Pantanal Barão de Melgaço Sub-Region	Pantanal	Brazil	camera-trapping	**0.58** ± 0.11	Trolle *et al.* (2007)
Private Ranches Paraguay River Basin	Cerrado-Pantanal Transition	Brazil	line transect (diurnal) camera-trapping	**2.04-2.34** (2 study areas)	Tarcísio Santos Jr. (unpublished results)
Kaa-Iya del Gran Chaco National Park	Chaco	Bolivia	VHF radio-telemetry (12 months)	**0.50**	Ayala (2003)
Kaa-Iya del Gran Chaco National Park	Chaco	Bolivia	camera-trapping	**0.22-0.80** (4 study areas)	Noss *et al.* (2003)
Kaa-Iya del Gran Chaco National Park	Chaco	Bolivia	VHF radio-telemetry (29 months)	0.26-**0.71**-1.16	Noss *et al.* (2003)
Guatopo National Park, Llanos	Llanos	Venezuela		**0.6** (crude) **0.8** (ecological)	Eisenberg *et al.* (1989)
The Density and Biomass of Tropical Mammals				**0.53**	Eisenberg (1980)
Neotropical forests				**1.60** +/- 2.6	Robinson & Redford (1986)
Neotropical forests				**1.60**	Robinson & Redford (1991)

2.2.4.5 Social Behaviour and Activity Patterns

Tapirs are shy, silent and very difficult to see due to their inconspicuousness in dense forested habitats. Tapirs are primarily solitary, and aside from a courting pair or a mother and her young, tapirs usually travel and feed alone (Eisenberg 1997). However, adults with juveniles or feeding groups are not completely unusual (Terwilliger 1978; Williams 1984; Eisenberg 1989; Eisenberg 1997). Data collected during this long-term tapir study in Morro do Diabo corroborates these observations. Through the use of nocturnal line-transect sampling for density estimates, I encountered tapirs in 81 occasions, of which 78% were solitary individuals. Only 12% of the encounters were of pairs of tapirs (adult female and adult male, or adult female with offspring), while three tapirs were sighted on one occasion. In one occasion, three tapirs were sighted. Among 36 lowland tapir sightings in Noel Kempff Mercado National Park, Bolivia, 86% were of solitary individuals and 14% were of male and female pairs (Herrera *et al.* 1999).

Tapirs are predominantly nocturnal and crepuscular. Noss *et al.* (2003) noted that lowland tapirs in Kaa-Iya del Gran Chaco National Park, Bolivia, were mostly active from 18:00-22:00 h, and from 24:00-06:00 h. In the same study area, Ayala (2003) observed that the main activity peak was from 01:00-06:30 h, with very little activity from 11:00-15:30 h. A camera-trap study in Madidi National Park, Bolivia, obtained 81 lowland tapir photos during night time, 11 during day time, and 8 during crepuscular periods (Gómez *et al.* 2005). Lowland tapirs at the Peruvian Amazon rested during the day and began their activity after sunset around 18:00 h, presenting activity peaks between 19:00-20:00 h and between 03:00-04:00 h, with the main foraging time from 21:00-03:00 h (Tobler 2008).

2.2.4.6 Reproduction

There is very little data about the reproduction of tapirs in the wild. Overall, tapirs have a very slow reproductive cycle. Adult female tapirs usually produce a single offspring after a lengthy gestation period from 13-14 months (390-410 days) (Barongi 1993). Twin births are very rare. Female tapirs are polyestrous with an oestrus cycle from 28-32 days. The oestrus period lasts from 1-4 days. Post partum oestrus is possible from 9-27 days after the calf is born. Thus, a female lowland tapir may conceive within a month after giving birth. In the wild, under ideal circumstances a young can be born every 14 months in habitats exhibiting little seasonality in food availability (Eisenberg 1997). In seasonally dry habitats, the interval between births may be longer. Inter-birth interval for captive lowland tapirs is can be as high as 18 months (Barongi 1993). Captive lowland tapirs are usually sexually mature by 14-24 months and conceive at an average of 4 years of age (Barongi 1993). The maximum age of reproduction for the species is 15 years for females and 19 years for males (D. Goff, AZA Lowland Tapir

Studbook Keeper, personal communication). Data on lowland tapir longevity comes from captivity and says that these animals live from 30-35 years (Barongi 1993). The generation length of wild lowland tapirs was estimated to be 11 years, considering age of first reproduction at 4 years and longevity of 25 years (Medici *et al.* 2007a; IUCN 2008a). Further data on lowland tapir reproductive rates and other life table parameters are discussed in Chapter 6.

2.2.4.7 Predators

Being such massive mammals, tapirs have very few natural predators. The main predators of lowland tapirs are jaguars (*Panthera onca*) and pumas (*Puma concolor*) (Hershkovitz 1954). Taber *et al.* (1997) recorded the presence of tapir remains in two jaguar scats among a total of 106 scat samples collected in the Paraguayan Chaco. Garla *et al.* (2001) collected 101 jaguar scats in the Atlantic Forests of Linhares Forest Preserve in Espírito Santo State, Brazil, and registered 0.7% of occurrence of lowland tapir remains. Astete *et al.* (2008) presented average frequencies of occurrence of tapir remains in jaguar scats in four Brazilian biomes: 0.4% in the Pantanal, 2.2% in the Atlantic Forest, 3.2% in the Amazon, and 4% in the Cerrado. During this 12-year field study on lowland tapirs in Morro do Diabo tapir predation by jaguar and puma was observed on several occasions. Three out of 25 radio-collared tapirs were predated by large cats. Two tapirs, one adult female and a sub-adult male, were predated by jaguar, while one sub-adult male tapir was predated by puma. Three carcasses of non-tagged adult tapirs killed by jaguars were found in different areas of Morro do Diabo during the study. Several of the captured tapirs presented scars, apparently from large cat attacks. Park rangers reported two sightings of jaguars chasing tapirs along the shoreline of the Paranapanema River. Jaguars and pumas usually attack tapirs at night when they leave the riverbanks and marshes to feed in the forest. Tapirs are able to walk away alive from such powerful predators due to the very thick skin around their neck, which is said to be 2-30 cm thick and very hard (when seizing and killing prey, the main target of a cat is the neck). In addition, tapirs have the ability to run off very fast through dense forest undergrowth, which may be a way of shaking off or out-running a predator.

2.2.5 Status and Threats

Globally, the lowland tapir is currently listed by IUCN - International Union for Conservation of Nature as "Vulnerable" under the criteria A2cde+3cde (IUCN 2008a; Schipper *et al.* 2008). The previous Red List assessment (IUCN 1996) listed lowland tapirs as "Lower Risk/Near Threatened". Therefore, the Red List status of the species has deteriorated over the past 12 years. Additionally, lowland tapirs are listed in CITES Appendix II (CITES 2005). Although the species is not included in the national list of species threatened with extinction in Brazil, it is reported in lists released recently by six states including Espírito Santo, Minas Gerais, Paraná, Rio de Janeiro, Rio Grande do Sul, and São Paulo. In Espírito Santo, Paraná, Rio de Janeiro, and São Paulo, it is listed as Endangered, and in Minas Gerais and Rio Grande do Sul, as Critically Endangered.

The tapir is one of the first species in its habitat to be adversely affected by human disturbance (Janzen 1981). The IUCN/SSC *Tapir Status Survey and Conservation Action Plan* identified habitat destruction and fragmentation, with resulting population isolation, and intensive hunting as the main factors behind the decline of lowland tapir populations throughout their geographic range (Brooks *et al.* 1997). Tapirs are among the preferred game species for subsistence and commercial hunters throughout the Amazon (Redford & Robinson 1991; Vickers 1991; Bodmer 1995; Bodmer & Lozano 2001). Estimates of lowland tapir harvest in the State of Loreto in the Peruvian Amazon range from 15,447-17,886 individuals per year (Bodmer 1995). Due to their individualistic lifestyle, low reproduction rate, long generation time, and relatively low population density, lowland tapirs do not achieve a high local abundance, which makes them highly susceptible to overhunting, and populations show rapid decline when harvested (Robinson & Redford 1986; Robinson & Redford 1991; Peres 1996; Bodmer *et al.* 1997; Cullen 1997; Cullen *et al.* 2000; Novaro *et al.* 2000; Peres 2000; Medici *et al.* 2007a). Another issue mentioned by Brooks *et al.* (1997) is that many lowland tapir populations are found outside the boundaries of legally protected areas, which hinders their protection.

A threat analysis carried out during the Lowland Tapir Population and Habitat Viability Assessment (PHVA) Workshop identified the main threats for each of the 21 different biomes where lowland tapirs occur (Medici *et al.* 2007a). Thirteen threats were identified including: hunting, habitat deforestation and/or alteration, resource extraction, habitat fragmentation (resulting in small populations and low connectivity), cattle ranching, infectious diseases, road-kill, fire, human density, plantations of monocultures, lack of patrolling in protected areas, small size of protected areas, and impact of tourism. For each biome, threats were ranked according to their severity into High, Medium, Low, or Non-Applicable, when the threat did not apply or when information on the threat was lacking (Table 2.8). A ranking of threats made specifically for the Atlantic Forest of the Interior suggests that the main threat for tapirs in this region is habitat fragmentation, closely followed by hunting pressure (Table 2.9). Other important threats for the region are habitat deforestation and/or alteration, cattle ranching, resource extraction, and road-kill. Plantation of monocultures also appears to be an important threat, which is mostly related to the expansion of soybean and sugar cane industries (Medici *et al.* 2007a).

Table 2.8. Threat analysis for 21 biomes where lowland tapirs occur (HUN: hunting; HDA: habitat deforestation, alteration; REX: resource extraction; FSP: habitat fragmentation, small populations; CR: cattle ranching; DIS: disease; RK: road-kill). Extracted from the Lowland Tapir Population and Habitat Viability Assessment (PHVA) Workshop Final Report (Medici *et al.* 2007a).

General Biomes	**HUN**	**HDA**	**REX**	**FSP**	**CR**	**DIS**	**RK**
North Eastern Amazon	X						
South Eastern Amazon			X	X	X		
Upper Amazon	X	X	X		X		
Amazonian Savannas		X					
Dry Chaco	X	X	X	X	X		
Humid Chaco	X		X	X	X		
Subtropical Andean Forests	X	X	X	X	X		
Llanos	X	X	X	X	X		X
Atlantic Forest of the Interior	X	X	X	X	X	X	X
Pantanal		X			X	X	X
Yunga Forests	X			X	X		
Brazilian Biomes	**HUN**	**HDA**	**REX**	**FSP**	**CR**	**DIS**	**RK**
Araucária Forests			X			X	
Cerrado	X	X	X	X	X	X	
Coastal Atlantic Forest	X	X	X	X			
Colombian Biomes	**HUN**	**HDA**	**REX**	**FSP**	**CR**	**DIS**	**RK**
Oriental Amazon	X	X	X	X	X		
Occidental Amazon	X	X	X	X			
Orinoquía	X	X	X	X	X		
Northeast Antioqueño	X	X	X	X	X		
Sierra Nevada de Santa Marta	X	X	X	X	X		X
Suriname Biomes	**HUN**	**HDA**	**REX**	**FSP**	**CR**	**DIS**	**RK**
Coastal Forests	X	X	X		X		
Venezuelan Biomes	**HUN**	**HDA**	**REX**	**FSP**	**CR**	**DIS**	**RK**
Northern Andes	X	X	X	X	X		

Table 2.9. Ranking of lowland tapir threats for the Atlantic Forest of the Interior, Brazil. Extracted from the Lowland Tapir Population and Habitat Viability Assessment (PHVA) Workshop Final Report (Medici *et al.* 2007a).

Threats	**Ranking**
Habitat fragmentation (resulting in small populations and low connectivity)	13
Hunting	12
Habitat deforestation and/or alteration	9
Cattle ranching	7
Resource extraction	5
Road-kill	4
Plantations of monocultures	2
Human density	1
Lack of patrolling in protected areas	1
Small size of protected areas	1
Infectious diseases	1
Fire	0
Impact of tourism	0

2.3 The Atlantic Forest Biome

2.3.1 Historical Outline

When Africa and South America split apart some 100 Million years ago, the Brazilian shield was exposed as a series of ridges running parallel to the new coast. It was upon these mountains of Precambrian stone, lashed by southern Atlantic trade winds that the Atlantic Forest evolved (Dean 1997; Câmara 2003). Despite the long period of geological stability that followed the separation of the continents, climatic change caused the forest to repeatedly expand and retract affecting the course of the biome's evolution and driving species differentiation (Whitmore & Prance 1987; Dean 1997).

In historical times, the Atlantic Forest stretched almost continuously for 4,000 km along the eastern Brazilian coast from Rio Grande do Norte State at the easternmost tip of the South American continent to as far as Rio Grande do Sul, the southernmost Brazilian state (Eiten 1970; Collins 1990; Dean 1997; Morellato & Haddad 2000; SOS Mata Atlântica & INPE 2008) and extending inland into eastern Paraguay and north eastern Argentina. The original size of the biome remains unclear because the Europeans, and later the Brazilians, altered so much of the landscape before the advent of scientific recording (Dean 1997). Nevertheless, a recent study by Ribeiro *et al.* (2009) mapped and estimated the original extent of the Atlantic Forest biome in Brazil to be 1.4 million km^2. Sanjurjo & Gauto (1996) estimated the original Atlantic Forest cover in Paraguay at 93,888 km^2, while Cartes (2003) gives a lower estimate of 88,050 km^2. Giraudo *et al.* (2003) estimated the original size of the Argentine Atlantic Forest to be 26,450 km^2. The sum of these estimates, using the broadest definition of the biome, gives a total area of ~1.5 million km^2.

The destruction of the Atlantic Forest and its wildlife began in the early 1500's, when the Portuguese first reached Brazil, beginning the European colonisation in the eastern part of South America (Dean 1997). The Atlantic Forest was cleared mainly for timber, firewood, charcoal, agriculture, cattle ranching, and the construction of cities (Morellato & Haddad 2000). Since the start of the century, crop and pasture lands have steadily expanded (Fonseca 1985) and the Atlantic Forests were rapidly converted to anthropogenic systems (Brown & Brown 1992; Coimbra-Filho & Câmara 1996; Dean 1997). As a result of its geographical location, the coastal region of the Atlantic Forest was the first to be exploited (Fonseca 1985). Ports and trading posts were established all along the coast, especially in Bahia and Rio de Janeiro states, and provided the first routes of penetration inland. Large-scale human settlements followed and agriculture became the most important economic activity in the region (Val 1972). The fertile lands of the coastal plains were first used for sugar cane, and supplying Europe with sugar rapidly became a major economic activity in the colony in the

16th and 17th centuries (Burns 1980). Coffee plantations developed in the 19th and 20th centuries. The logging of the Pau-Brasil tree (*Caesalpinia echinata*) was another important economic activity (Dean 1997). This process of occupation of the Atlantic Forest, marked by centuries of unsustainable use, caused a drastic reduction of this biome (Galindo-Leal & Câmara 2003).

2.3.2 Ecological Outline

Despite their high level of endangerment, Atlantic Forests make up the second largest tropical moist forest area of South America, after the vast Amazonian domain. The Atlantic Forest extends from 4-32°S and covers a wide range of climatic belts and vegetation formations, from tropical to subtropical. Elevation ranges from sea level to 2,900 masl, with abrupt changes in soil type and depth and average air temperature (Mantovani 2003). Longitudinal variation is also marked. The Atlantic Forest is extremely heterogeneous in composition and includes very complex natural landscapes (Oliveira-Filho & Fontes 2000).

The Atlantic Forest domain can be subdivided into two major regions based on its vegetation types and geographical features (Mori *et al.* 1981; Morellato & Haddad 2000). The first vegetation type is classified as Tropical Evergreen Mesophytic Broadleaf Forest or Atlantic Rain Forest *sensu stricto*. The second vegetation type is the Tropical Semi-Deciduous Mesophytic Broadleaf Forest or Semi-Deciduous Atlantic Forest *sensu lato*, also known as Atlantic Forest of the Interior, where this study took place.

The Atlantic Rain Forest covers mostly the low to medium elevations (≤1,000 masl) of the eastern slopes of the mountain chain (*Serra do Mar*) that runs along the coastline from southern to north eastern Brazil (Eiten 1970). The Atlantic Rain Forest comprises only the coastal rain forests up to 300 km inland, where rainfall is locally boosted by oceanic winds and seaside mountain ranges. It is one of the most spectacular forests growing under a tropical wet climate. The Semi-Deciduous Atlantic Forest extends across the western range of the coastal hills, stretching to the *Plateau* region (*Mata de Planalto*, usually ≥600 masl in elevation) in the centre and south eastern interior of Brazil and stretching into Paraguay and Argentina (Leitão-Filho & Morellato 1997; Oliveira-Filho & Fontes 2000). The Atlantic Rain Forest experiences high mean annual temperatures (16-19°C) and ever-wet forest climate with annual precipitation from 2,000-4,000 mm and without a dry season. An increasingly seasonal climate with average annual rainfall dropping from 4,000-1,000 mm and a relatively severe dry season, generally from April to September, corresponding to the winter season, predominates over the distribution of the Semi-Deciduous Atlantic Forest (Morellato *et al.* 2000; Oliveira-Filho & Fontes 2000; Mantovani 2003).

The broad view of Atlantic Forest *sensu lato* attaches semi-deciduous forests to coastal Atlantic Rain Forests, pushing the limits of the Atlantic Forest domain up to 700 km inward from the coast (Fernandes & Bezerra 1990). The Federal Decree 750/1993 defines the Atlantic Forest vegetation as "the formations and associated ecosystems inserted in the Atlantic Forest domain, with the following delimitations established by the Brazilian Vegetation Map (IBGE 1988): ombrophilous dense Atlantic Forests; mixed ombrophilous forests; open ombrophilous forests; semidecidual stational forests; decidual stational forests; the countryside swamps, the north eastern forest enclaves and the associated ecosystems - mangroves and *restingas*."

This definition of Atlantic Forests has become widely accepted (CEPF 2002). However, as might be expected for a vast and diversified vegetation province, the classification and geographic distribution of the Atlantic Forest is still a matter of controversy (Câmara 1991; Oliveira-Filho & Fontes 2000). Fixing inland limits to the Atlantic Forest domain is very complicated, since their transition to the hinterland open formations is very complex and gradual. This transition can be classified into three regions according to the adjacent open formation (Oliveira-Filho & Fontes 2000). A relatively abrupt transition to the semiarid Caatingas occurs in north eastern Brazil where a narrow strip (50 km) of coastal Atlantic Rain Forest is bordered by an equally narrow inland belt of seasonal semi-deciduous forests (Andrade-Lima 1982). The transition between coastal Atlantic Forest and the Cerrado in south eastern Brazil involves a much larger extent of semi-deciduous forests that becomes increasingly wide toward the south and forms complex mosaics with Cerrado vegetation to the west. These semi-deciduous forests also stretch southward along the Paraná River basin into eastern Paraguay and north eastern Argentina where they are transitional to the Chaco biome. A number of associated formations include mangroves, *restingas* (coastal scrub forest on sandy soils), high-elevation grasslands (*campo rupestre*), and *brejos* (humid forests resulting from orographic rainfall in otherwise semi desert scrub in the northeast of Brazil) (Câmara 2003). For academics and conservationists supporting the Atlantic Forest *sensu stricto*, the neighbouring semi-deciduous forests are a distinct vegetation formation, known as *Matas de Planalto* (Plateau Forests), due to their distribution on the hinterland highlands. The flora of semi-deciduous forests is considered by many as either transitional between that of Atlantic Rain Forests and Cerrado or part of a continuum of forest species distribution that includes central Brazilian gallery forests that eventually links Atlantic to Amazonian forests (Oliveira-Filho & Ratter 1995).

2.3.3 Current Conservation Status

The year 2000 marked 500 years of destruction of the Atlantic Forest in all three countries of occurrence - Argentina, Brazil, and Paraguay - which is seen as one of the most alarming conservation problems in the world (Mori *et al.* 1981; Terborgh 1992; Viana *et al.* 1997). The original extent of the Atlantic Forest biome in Brazil, including forests, mangroves and *restingas*, has been reduced by ~88% (Ribeiro *et al.* 2009). The remaining forest cover ranges from 11-16%, which is actually more than previously estimated (Ribeiro *et al.* 2009). Further estimates of the original cover and remaining forest cover of the Atlantic Forest biome in Brazil, Argentina and Paraguay are shown in Table 2.10.

Approximately 70% of Brazil's 184 million people are concentrated in 3,000 cities built on cleared lands of the Atlantic Forest, even though it accounts for only 11% of the nation's territory (Fonseca 1985; Chiarello 1999). Some of these cities are among the largest in Latin America and in the world, such as São Paulo and Rio de Janeiro, the main industrial poles in the country. About 80% of the Brazilian GDP is generated in the Atlantic Forest region. The remaining Atlantic Forest consists of small and isolated forest islands scattered throughout a landscape dominated by agricultural uses and urban development (Fonseca 1985; Morellato & Haddad 2000). According to Ribeiro *et al.* (2009), the Brazilian Atlantic Forest is currently distributed in 245,173 forest fragments. The best-preserved bio-geographical sub-region is the *Serra do Mar* along the coast, which holds ~36% of its original vegetation. The largest Atlantic Forest fragment (11,095 km^2), as well as the second- and third-largest fragments, are indeed located in the Serra do Mar. Altogether, these three fragments account for more than 20,000 km^2 or 13% of the remaining forest. In contrast, 83% of the remaining Atlantic Forest fragments are smaller than 0.5 km^2, and together they account for 31,780 km^2 or 20% of the total forest. The fragments smaller than 2.5 km^2 represent more than 97% of the total number, and account for almost 42% of the total forest cover. Only 77 fragments are larger than 100 km^2 (Ribeiro *et al.* 2009).

Table 2.10. Past and present extent of the Atlantic Forest, extracted from Flesher (2007).

Original Cover (km^2)	**Amount Remaining** (km^2)	**% of Original Cover**	**Reference**	**Comments**
1-1,500,000	20,000-90,000	2-10	Por (1992)	ENTIRE BIOME
1,500,000	120,000	8	Galindo-Leal & Câmara (2003)	ENTIRE BIOME
1,205,780	146,024	12	Brown & Brown (1992)	BRAZIL
1,000,000		<10	Dean (1997)	BRAZIL
1,090,000 1,250,000	100,000 130,000	9.2 10.4	Fearnside (1996) SOS Mata Atlântica (1992)	BRAZIL *Top number excludes Araucária forests*
1,227,600	91,930	7.5	Myers *et al.* (2000)	BRAZIL
1,350,000	216,623	17	SOS Mata Atlântica & INPE (2002)	BRAZIL
1,306,421	98,878	7.25	Câmara (2003)	BRAZIL
1,395,849	163,775	11.4-16	Ribeiro *et al.* (2009)	BRAZIL
93,888	47,488	51	Sanjurjo & Gauto (1996)	PARAGUAY *11,827 km^2 of degraded lowland forest*
88,050	11,618	13.2	Cartes (2003)	PARAGUAY
26,450	11,303	44	Giraudo *et al.* (2003)	ARGENTINE

Despite severe legal restrictions on deforestation in Brazil, the Atlantic Forest is still under severe anthropogenic pressure, and suffers from various patterns of habitat fragmentation. The rate of forest loss is still high, approaching 350 km^2 or 0.25% $year^{-1}$ (SOS Mata Atlântica & INPE 2008). The remaining Atlantic Forest fragments are threatened in all three countries of occurrence by logging, deforestation driven by agriculture and expansion of pasture land for cattle ranching, cutting of firewood, forest fires, poaching and animal trading, urban and industrial development, construction of infrastructure such as roads and dams, and uncontrolled tourism (CEPF 2002). In addition, the establishment of agrarian reform settlements that use unsustainable land-use practices within their boundaries or in adjacent areas is a problem (Cullen *et al.* 2005).

Most of the Atlantic Forest remnants are privately owned, and their fate is highly dependent upon the attitudes of farmers and local communities (Viana *et al.* 1997). Many of these areas are not effectively protected, and their land tenure is unresolved (Furlan *et al.* 2000). No more than 3% of the Atlantic Forest occurs within protected areas, and only one-quarter of all protected areas remaining in the Atlantic Forest are large enough to sustain viable animal populations (Chiarello 2000). Nevertheless, these remaining 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 (Tabarelli *et al.* 2003).

The Atlantic Forest biome is a global conservation priority as it harbours one of the highest plant and vertebrate diversity on Earth, containing nearly 8% of the world's total species, many of which are endemic to this biome and/or threatened with extinction (Myers *et al.* 2000; Brooks *et al.* 2002; Galindo-Leal & Câmara 2003; Ceballos & Ehrlich 2006). A recent assessment of the Atlantic Forest highlighted the large number of endemic species in several groups, such as 8,000 tree species (40% of the total), 200 birds (16%), 71 mammals (27%), 94 reptiles (31%), and 286 amphibians (60%), to mention only the best-known taxonomic groups (Mittermeier *et al.* 2005). The degree of mammal endemism in the Atlantic Forest, estimated at 27%, is exceeded only by the Amazon, in which 59% of its total mammal fauna restricted to that biome. The high level of endemism among Atlantic Forest mammal species is mainly due to three orders: marsupials, rodents, and primates, which together comprise 84% of all endemics (Pires-Costa *et al.* 2000). More than two thirds of the primate species found in the Atlantic Forest is endemic to this biome (CEPF 2002).

Most species officially threatened with extinction in Brazil are inhabitants of the Atlantic Forest (Tabarelli *et al.* 2003). Currently, more than 530 species of plants, birds, mammals, reptiles, and amphibians of the Atlantic Forest are threatened—some at the biome level, some at the country level, and the endemic species, at the global level. At least 158 species of birds of the

Atlantic Forest are Critically Endangered (Ferraz *et al.* 2007). Of 24 species of primates occurring in the Atlantic Forest, 22 are threatened and restricted to small fragments, where long-term survival is unlikely (Pires-Costa *et al.* 2005). Forest destruction has resulted in the elimination of many populations, and potentially, in the erosion of the genetic diversity of several species (Brown & Brown 1992; Ribon *et al.* 2003). Based on the nearly total destruction of this biome and the high number of endemic species specialised to the forest environment, it is reasonable to suppose that many species have already gone extinct before they were described (Morellato & Haddad 2000). It is reasonable to speculate that as global warming occurs and habitats change, this already alarming number of threatened species will increase because the widespread fragmentation of the Atlantic Forest limits species migration and colonisation necessary for the long-term persistence of populations (Tabarelli *et al.* 2005).

Consequently, the Atlantic Forest is considered a "hotspot" for biodiversity conservation (Myers *et al.* 2000). Myers (1988) identified 10 tropical forest "hotspots" characterised both by exceptional levels of plant endemism and by extensive habitat loss. In 1989, Conservation International adopted Myers' hotspots as its institutional blueprint. Three years later an extensive global review was undertaken, which introduced quantitative thresholds for the designation of hotspots. To qualify, a hotspot must contain at least 1,500 species of vascular plants as endemics, and it has to have lost at least 70% of its original habitat. Twenty-five biodiversity hotspots were identified and the Atlantic Forest was classified as the 4th hottest hotspot, demonstrating its conservation priority (Mittermeier *et al.* 1999; Myers *et al.* 2000).

Likewise, the Atlantic Forest is among the 867 defined terrestrial Ecoregions defined by the World Wildlife Fund (Olson *et al.* 2001). Ecoregions are defined as large areas of relatively uniform climate that can harbour a characteristic set of species and ecological communities (Bailey 1998). 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 habitats. WWF's Global Ecoregions Program is the first comparative analysis of terrestrial biodiversity to cover every major habitat type in five continents (Olson *et al.* 2001). The Ecoregion concept also provides a blueprint for biodiversity conservation at a global scale, ensuring that the full range of ecosystems is represented within regional conservation strategies (Grooves 2003).

2.4 The Atlantic Forest of the Interior and the Pontal do Paranapanema Region

The Atlantic Forest of the Interior is included in the Federal Decree n°750 of 1993 that legally defines the geographical domains of the Atlantic Forest biome in Brazil and regulates its use (Valladares-Padua *et al.* 2002). Approximately 22,000 km^2 of the Atlantic Forest of the Interior remains in the Plateau region of Brazil (SOS Mata Atlântica & INPE 2008); 11,303 km^2 lies in Argentina, where it stretches as a contiguous corridor covering a large part of the province of Missiones (Di Bitetti *et al.* 2003; Giraudo *et al.* 2003); and 11,618 km^2 lies in Paraguay (Cartes 2003). The Atlantic Forest of the Interior has been extremely fragmented, mostly due to agricultural and industrial expansion, resulting in the loss of more than 98% of its forests (Dean 1997; SOS Mata Atlântica & INPE 2008). Some of the most significant remnants of the Atlantic Forest of the Interior in Brazil are found in the Pontal do Paranapanema Region, a wedge-shaped region bounded in the south by the Paranapanema River (22°27'-22°40'S) and in the west by the Paraná River (52°10'-52°22'W), marking the westernmost extremity of São Paulo State (Figure 2.5).

The history of the Pontal do Paranapanema Region is marked by land disputes and conflicts. In 1941, while still entirely forested, the entire western part of São Paulo, comprising an area of ~2,600 km^2, was decreed a forest reserve, the "*Grande Reserva do Pontal*" (Great Reserve of the Pontal do Paranapanema) (Valladares-Padua 1993; Leite 1998) (Figure 2.5). However, it was never formally protected. In the same year, Morro do Diabo State Reserve was legally created through the Federal Decree nº12.278 (Schlittler 1990). During the 1950's, the State Governor Ademar de Barros distributed large parts of the "Grande Reserva" to his friends and allies. This rapidly initiated a wave of deforestation as a means to guarantee their ownership and forestall any future attempts to return it to its status of wildlife reserve (Valladares-Padua *et al.* 2002). In 1986, Morro do Diabo was decreed a state park (Decree nº25.342), consisting of the largest remaining area of native forest in the western portion of São Paulo.

In the mid 1990's, large cattle ranches, which had been carved out of the "Grande Reserva" during the 1950's, 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) (Cullen 2007). These lands were later expropriated for public land reform settlements by the São Paulo State Institute of Agrarian Reform (ITESP). ITESP subdivided the land for thousands of landless settlers coming from many different parts of the country, dramatically increasing the human density in the region (Cullen 2007). Over 5,000 landless families have been settled in the Pontal do Paranapanema Region and are now farming along forest edges (Cullen *et al.* 2005).

As a result of all the conflicts over land ownership and widespread destruction of the forests of the Pontal do Paranapanema Region during the last 60 years, less than 2% of the "Grande Reserva" remained (Dean 1997). Deforestation in the Pontal from 1987-2001 occurred at a rate of 1.5% year^{-1} (Cullen 2007). Interestingly, the process of deforestation of the Pontal do Paranapanema Region is relatively recent in the history of destruction of the Atlantic Forest when compared to areas in the eastern part of the biome.

Nevertheless, the Pontal do Paranapanema Region alone still comprises 84% of the remaining Plateau forest cover, mostly in a single patch - Morro do Diabo State Park - which protects 370 km^2 of forest (Figure 2.6). In July 2002, the Federal Government of Brazil declared the creation of another protected area in the region, the Black-Lion-Tamarin Ecological Station, comprising an additional 67 km^2 of protected habitat in the Pontal do Paranapanema Region. The Black-Lion-Tamarin Ecological Station encompasses the four largest forest fragments situated around Morro do Diabo - Santa Maria Cachoeirinha, Tucano, Ponte Branca, and Água Sumida Estrela da Alcídia - and is under the administration of IBAMA - Instituto Brasileiro do Meio Ambiente e Recursos Naturais Renováveis. Small forest fragments from 0.02-20 km^2 are scattered around both protected areas, adding up to a further 60 km^2 of forest (Ditt 2002; Uezu *et al.* 2008). Most of these non-protected forest remnants lie within private properties but some are located in landless settlements and are owned by the State. Some of the remaining forests still exist due to the Brazilian law that requires properties within the legal geographical domain of the Atlantic Forest to maintain at least 20% of their land covered with original forests (*Reserva Legal*) (Cullen *et al.* 2001b). According to Uezu *et al.* (2008), 17% of the Pontal do Paranapanema Region is still covered with forests. The landscape matrix is mainly composed of pasture land (60%) and agriculture (15%) (Uezu *et al.* 2008).

Because of the extensive loss of forest, the conservation of the forest remnants of the Pontal do Paranapanema Region is of utmost importance, as they still harbour the rich and endemic biodiversity of the region, and many of its endangered species. The biological value of even the small remaining Atlantic Forest fragments is unquestionable. Although most of these forest fragments are very small and degraded, they still support an outstanding diversity of species of flora and fauna of the Atlantic Forest of the Interior.

These forest patches provide habitats for a wide variety of species that disperse and pollinate native vegetation, increasing regional genetic flow. These patches also represent the only and last remaining "seed banks" for these endangered ecosystems that can be used for forest restoration programs and landscape linkages. Most importantly, these forest patches serve as "stepping-stones," or small patches of native forest that increase connectivity among forest fragments facilitating the dispersal of organisms (Cullen *et al.* 2001b).

Figure 2.5. Reference maps indicating the location of the Pontal do Paranapanema Region in the extreme western portion of São Paulo State, Brazil. Lower map indicates the historic range of the "Great Reserve of the Pontal do Paranapanema" and the current location of Morro do Diabo State Park (Devil´s Hill State Park). Sketch maps designed by Anders Gonçalves da Silva.

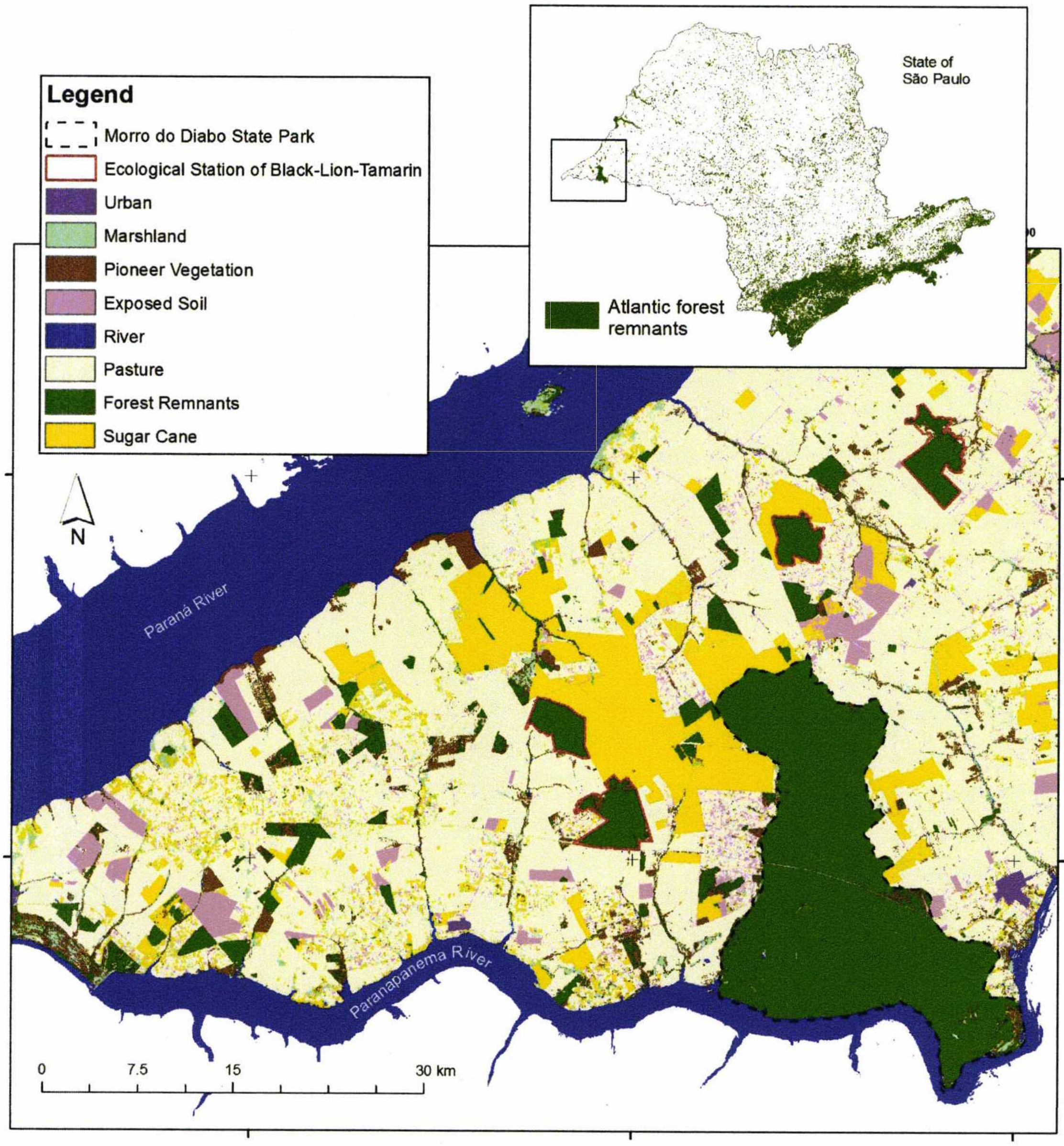


Figure 2.6. Map of the Pontal do Paranapanema Region indicating Morro do Diabo State Park, Black-Lion-Tamarin Ecological Station, and other remaining forest fragments in the surroundings. The Black-Lion-Tamarin Ecological Station encompasses the four largest forest fragments situated around Morro do Diabo. Map designed by Alexandre Uezu.

2.5 Study Site: Morro do Diabo State Park

2.5.1 Location and Legal Protection

Morro do Diabo State Park (Devil's Hill State Park) is located in the southern part of the Pontal do Paranapanema Region, São Paulo State (22°16'-22°40'S; 52°05'-52°30'W), and protects 370 km^2 of the Atlantic Forest of the Interior. Morro do Diabo is administered by the Forestry Institute of São Paulo State (*Instituto Florestal do Estado de São Paulo*). Morro do Diabo is well protected with legally demarcated, undisputed boundaries.

2.5.2 Landscape Matrix

The landscape matrix around Morro do Diabo is mainly composed of pasture land and agriculture. The great majority of the properties surrounding Morro do Diabo and the other forest fragments in the Pontal do Paranapanema Region are very small. Most of these properties have been distributed to hundreds of landless families as part of a country-wide programme of Agrarian Reform. Most of the Agrarian Reform settlements are located near the western and northern borders of Morro do Diabo. Most of the landscape matrix in between forest fragments consists of pasture land for cattle ranching and agricultural crops such as sugar cane, manioc, corn, and cotton. Sugar cane plantations dominate the landscape near the north western and north eastern borders of Morro do Diabo. Cattle ranching is the main activity in the south eastern border.

The Paranapanema River, a large, wide river and the main permanent source of water in the area, runs along the southern limit of Morro do Diabo. The Ribeirão Bonito stream, a very important source of water for wildlife in Morro do Diabo, runs along the entire western edge of Morro do Diabo. The vegetation along the Ribeirão Bonito stream is characterised by several islands of swamp vegetation and patches of humid fields, both surrounded by riparian forests. The other water courses in Morro do Diabo are small streams that during extreme dry seasons have their levels of water considerably reduced.

2.5.3 Climate

The climate in the Pontal do Paranapanema Region is Cfa, following the Köppen classification. Winters are cold and dry, and temperatures range from 15-20°C, and summers are hot and humid, with temperatures as high as 40°C. The average annual temperature is ~22°C. The region is characterised by a pronounced dry season (April-September). Annual rainfall is 1,347 mm, of which about 70% falls during the wet season (October-March) (Faria & Pires 2006) (Table 2.11).

Table 2.11. Monthly temperature (°C), relative humidity (%), and rainfall (mm) in Morro do Diabo State Park, São Paulo, Brazil. Data gathered from 1977-2002 (Faria & Pires 2006).

Month	Temperature			Relative Humidity			Monthly Rainfall (mm)
	Min (°C)	Mean (°C)	Max (°C)	Min (%)	Mean (%)	Max (%)	
Jan	20.7	25.3	32.3	57	82	92	132
Feb	20.5	25.3	32.8	58	82	94	156
Mar	19.7	24.6	32.3	57	80	94	128
Apr	17.4	22.5	30.3	56	82	95	85
May	13.6	19.1	26.9	57	85	96	103
Jun	11.1	17.2	25.4	54	85	96	72
Jul	11.5	17.5	26.5	48	81	94	37
Aug	12.1	18.8	27.9	45	77	92	50
Sep	14.2	20.1	27.6	50	77	90	118
Oct	17.0	23.1	31.1	50	77	90	129
Nov	18.6	24.2	31.6	51	78	90	125
Dec	19.9	25.1	32.0	57	80	92	212
Total							**1,347**
MEAN	16.4	**21.9**	29.7	53	81	93	**112**
MAX	20.7	25.3	32.8	58	85	96	212
MIN	11.1	17.2	25.4	45	77	90	37

2.5.4 Abiotic Factors

The average altitude in Morro do Diabo State Park is ~320 masl. The Pontal do Paranapanema Region is characterised by open hills, with gentle slopes less than 15% (Ross & Moroz 1997), with exception of Devil's Hill itself, which has an elevation of ~570 m. The region is known for its nutrient-poor soils, which are for the most part sandy dark-red latosols and oxisols (Setzer 1949; Schlittler 1990; Oliveira *et al.* 1999).

2.5.5 Biotic Factors

2.5.5.1 Fauna

The Morro do Diabo State Park Management Plan (Faria & Pires 2006) includes lists of mammals, reptiles, amphibians, birds and fish found in Morro do Diabo and surrounding forest fragments in the Pontal do Paranapanema Region. These lists include 60 species of mammals, 53 reptiles, 15 amphibians, 288 birds, and 26 fishes. Carnivores include jaguar (*Panthera onca*), puma (*Puma concolor*), ocelot (*Leopardus pardalis*), margay (*Leopardus weidi*), crab-eating fox (*Cerdocyon thous*), coati (*Nasua nasua*), tayra (*Eira barbara*), and river-otter (*Lutra longicaudis*) among others. Primates include howler monkey (*Alouatta fusca*), capuchin monkey (*Cebus apella*), and the endangered black-lion-tamarin (*Leontopithecus chrysopygus*). The species of ungulates that occur in Morro do Diabo are white-lipped peccaries (*Tayassu pecari),* collared peccaries (*Pecari tajacu),* red-brocket deer (*Mazama americana*), gray-brocket deer (*Mazama gouazoubira*), and lowland tapir (*Tapirus terrestris*).

2.5.5.2 Flora

According to the official classification by IBGE - Instituto Brasileiro de Geografia e Estatística (Brazilian Institute of Geography and Statistics), Morro do Diabo State Park is the largest single remnant of Seasonal Tropical Semi-Deciduous Forest (Atlantic Forest of the Interior) in the State of São Paulo (IBGE 1988; Veloso *et al.* 1991; Oliveira-Filho & Fontes 2000). Most of the emergent trees lose from 20 to 50% of their leaves during the dry season (Hueck 1972). The forests of Morro do Diabo are considered a transitional ecosystem, bordered by tropical evergreen broadleaf forests to the east, which originally covered the Atlantic coastline, and the dry Cerrado vegetation to the north and west (Ab'Saber 1977). Durigan & Franco (2006) provided detailed descriptions of the flora of the Pontal do Paranapanema Region, including Morro do Diabo and surrounding forest fragments.

In 2006, the Forestry Institute of São Paulo State (*Instituto Florestal do Estado de São Paulo, Secretaria do Meio Ambiente*) and a number of partners including IPÊ - Instituto de Pesquisas Ecológicas - developed a Management Plan for Morro do Diabo (Faria & Pires 2006). The plan identified and mapped 10 different vegetation types found in Morro do Diabo, as well as in the forest fragments located within its designated buffer zone (Figure 2.7). Detailed descriptions of each vegetation type are provided below:

1) **Tall mature forest:** This vegetation type is mostly found in the southern part of Morro do Diabo. This forest type is crossed by several water courses and vegetation is exuberant. It includes key tree species such as *Gallesia integrifólia*, *Metrodorea nigra*, and *Bouganivillea glabra*, which suggest the occurrence of fertile soils in these areas. This forest type also presents high densities of species from the Lauraceae, Meliaceae, and Myrtaceae families. Campos & Heinsdijk (1970) estimated significant volumes of wood (54 m^3 ha^{-1}) in this forest, with high concentrations of hard wood trees such as *Aspidosperma polyneuron*, *Cedrella fissilis*, and *Balfourodendron riedelianum*. Schlittler (1990) carried out vegetation surveys in this area of Morro do Diabo and found a total density of 1,119 trees ha^{-1}, including 104 different tree species. The average height of these forests is ~15 m with the occurrence of emergent trees of up to 40 m in height. It is believed that the emergent trees survived forest fires in the past and the forest underneath is the result of secondary regeneration. There is a visible gradient of vegetation biomass in this forest type with the biomass increasing as the forest approaches the riparian forests along the Paranapanema River in the southern part of Morro do Diabo.

2) **Low mature forest:** This vegetation type is mostly found in the western part of Morro do Diabo, especially in areas close to water courses. The soil presents low levels

of fertility and permeability. The forest is low (~12 m), but presents a high density of plants. However, the vegetation biomass and volume of wood are lower than the values found for tall mature forest. Most of the trees found in this forest type belong to the Myrtaceae family, represented by a large number of species including *Myrcia multiflora*, *Myrcia fallax*, *Myrciaria cuspidata*, *Myrciaria ciliolata*, and *Eugenia* sp among others. Some species that are characteristic of the Cerrado biome have been identified in low densities in this forest type, including *Qualea cordata*, *Ouratea floribunda*, *Pera obovata*, *Roupala montana*, and *Tabebuia ochracea* among others. This forest type has low occurrence of lianas, which facilitates the penetration of light. On the other hand, the forest floor is mostly covered with Plumier (*Bromelia balansae*), a bromeliaed from the family Bromeliacea, which due to the large thorns on its leaves makes it very difficult to walk through this forest. Both the Myrtaceae and bromeliads provide abundant fruit for wildlife.

3) **Secondary forest in early stages of regeneration:** This vegetation type, also known as *Sapezal* (*Sapé* is a type of tall grass, *Imperata brasiliensis*, very susceptible to forest fires) or scrub grassland, was identified and described by Campos & Heinsdijk (1970). This vegetation occurs in a patch of ~10 km^2 in the eastern limits as well as in several small patches inside Morro do Diabo. The areas of *Sapezal* near the edges of Morro do Diabo have been affected by several fire events over the past 40 years. Most of the forest fragments surrounding Morro do Diabo have been classified within this vegetation type, which shows their level of degradation. In Morro do Diabo, the patches of *Sapezal* are slowly being occupied by the forests in their surroundings. Today, the *Sapezal* is reduced to ~10% of the original area it covered 40 years ago, and it is expected that this vegetation type will disappear over time. This vegetation type is mostly composed of *Sapé* grass and tree species of early stages of regeneration such as *Gochnatia polymorpha, Syagrus romanzoffiana, Platypodium elegans, Guarea guidonea, Casearia gossypiosperma* and *Didymopanax morototonii.*

4) **Secondary forest in late stages of regeneration:** This vegetation type comprises 10 km^2 or approximately one third of the area of Morro do Diabo. Campos & Heinsdijk (1970) estimated a volume of wood for this forest of ~26 m^3 ha^{-1}. This vegetation type is mostly found along the highway that crosses Morro do Diabo, as well as on the north eastern limits of Morro do Diabo. These areas have been impacted by several forest fires, and therefore present high densities of lianas forming a wall of vegetation that one cannot go through. Today, this vegetation type is described as a very diverse forest, with continuous tree canopy composed by young individuals of small size, resulting in low biomass. Emergent trees are very rare. This vegetation type also presents high concentrations of bamboo in the forest understory. There is a

predominance of tree species characteristic of early stages of regeneration such as *Gochnatia polymorpha, Croton floribundus, Helietta apiculata, Didymopanax morototonii,* and *Casearia gossypiosperma*. However, young individuals of several tree species characteristic of late stages of regeneration can also be found.

5) ***Cerrado* (Savannah):** This vegetation type is represented by a very small patch (0.034 km^2) of *Cerrado* with very low biomass of plants immersed in the middle of tall mature forests in the north western part of Morro do Diabo. This small island of *Cerrado* vegetation is of great value for the understanding of the dynamics of transition between *Cerrado* and forest. Satellite images show other small patches of savannah type vegetation (non-continuous canopy) in the north western part of Morro do Diabo, but this has yet to be confirmed through field expeditions to these areas. In this vegetation type, adult trees are very rare. Most plant species found in the area are typical of the *Cerrado* biome, including *Diospyros híspida* and *Anadenanthera falcata* with predominance of *Campomanesia adamantium, Duguetia furfuracea, Tallisia pygmaea, Byrsonima intermedia, Allagoptera campestris* and *Pradosia brevipes*. The high density of *Campomanesia adamantium* is a factor that attracts wildlife to this area during the fruiting season (November, December). The forest floor is covered with different species of grass as well as *Bromelia plumieri* and *Ananas ananassoides*. Two species of Cactaceae can be found in this vegetation type, *Cereus hildmanianus* and *Praecereus euchlorus*.

6) **Riparian forest along the Ribeirão Bonito Stream:** The Ribeirão Bonito stream runs along the western edge of Morro do Diabo. Although on the satellite images this vegetation type appears to be similar to the tall mature forest or *Sapezal*, the vegetation is very peculiar. It is characterised by a combination of islands of swamp forest (*Talauma ovata, Tabebuia umbellata, Styrax pohlii, Nectandra nitidula, Geonoma brevisphata, Cedrella odorata*) and humid fields surrounded by riparian forests including tree species less tolerant to wet soils such as *Endlicheria paniculata, Tapira guianensis, Eugenia speciosa* and *Ocotea corymbosa*. The result is a mosaic of vegetation types. This part of Morro do Diabo has several areas of ecological instability due to siltation of the Ribeirão Bonito stream caused by agricultural activities outside of Morro do Diabo.

7) **Riparian forest along the Paranapanema River:** Most of the vegetation that covered the areas along the Paranapanema River was submerged during the flooding of the Rosana Dam in 1987. The forest along the river was cleared before the flooding in order to reduce the amount of organic matter in the water of the reservoir. In some areas the clearing went too far beyond the pre-established elevations to be deforested

and those areas were never flooded. Today, these areas, especially the ones next to the headquarters of Morro do Diabo, are formed by a high concentration of exotic grasses, with predominance of *Panicum maximum* and sparse tree species in different stages of regeneration. In the humid areas, next to the river, there is a predominance of species that tolerate drenched soils such as *Croton urucurana, Inga vera* and *Psidium guajava*. In the dry areas, there is a predominance of species of legumes and pioneers, all colonisers or coming from the seed banks (*Peltophorum dubium, Trema micrantha, Croton floribundus, Solanum* spp among others). This vegetation type is currently going through the process of natural secondary regeneration, which is in great part limited by the proliferation of *Panicum maximum*. This grass obstructs the germination of seeds and development of trees, and increases the risk of forest fires.

8) **Low, dense forest in various stages of regeneration:** This vegetation type is also considered secondary forest in regeneration, presenting plant species in several stages of regeneration including pioneer species and species of the later stages of the regeneration process. The density of plants and the concentration of lianas are very high. Most of the patches of this vegetation type can be found along the highway that crosses Morro do Diabo, as well as along the old, deactivated railroad that goes through Morro do Diabo.

9) **Temporary lakes:** There are some areas in the southern part of Morro do Diabo that appear on satellite images sometimes as water and sometimes as herbaceous vegetation. These patches are temporary lakes that dry out during the dry season, becoming a field of different species of grass and sedges (Cyperaceous plants) from 50-100 cm of height. In the edges of these lakes, where the terrain has better drainage, tree species such as *Sebastiania klotzchyana* and *Copaifera langsdorffii* can be found, however, the colonisation by tree species is certainly limited by the drainage of the soil during the wet season.

10) **Agricultural and pastoral land:** This includes areas of agriculture and pasture for cattle ranching in the farms and ranches located in the surroundings of Morro do Diabo, outside the boundaries of the protected area. Some of the most important, traditional agricultural crops in the Pontal do Paranapanema Region are sugar cane, corn, cotton, and manioc among others. Most of the pastures in the region are composed of exotic grasses, especially *Brachiaria* spp.

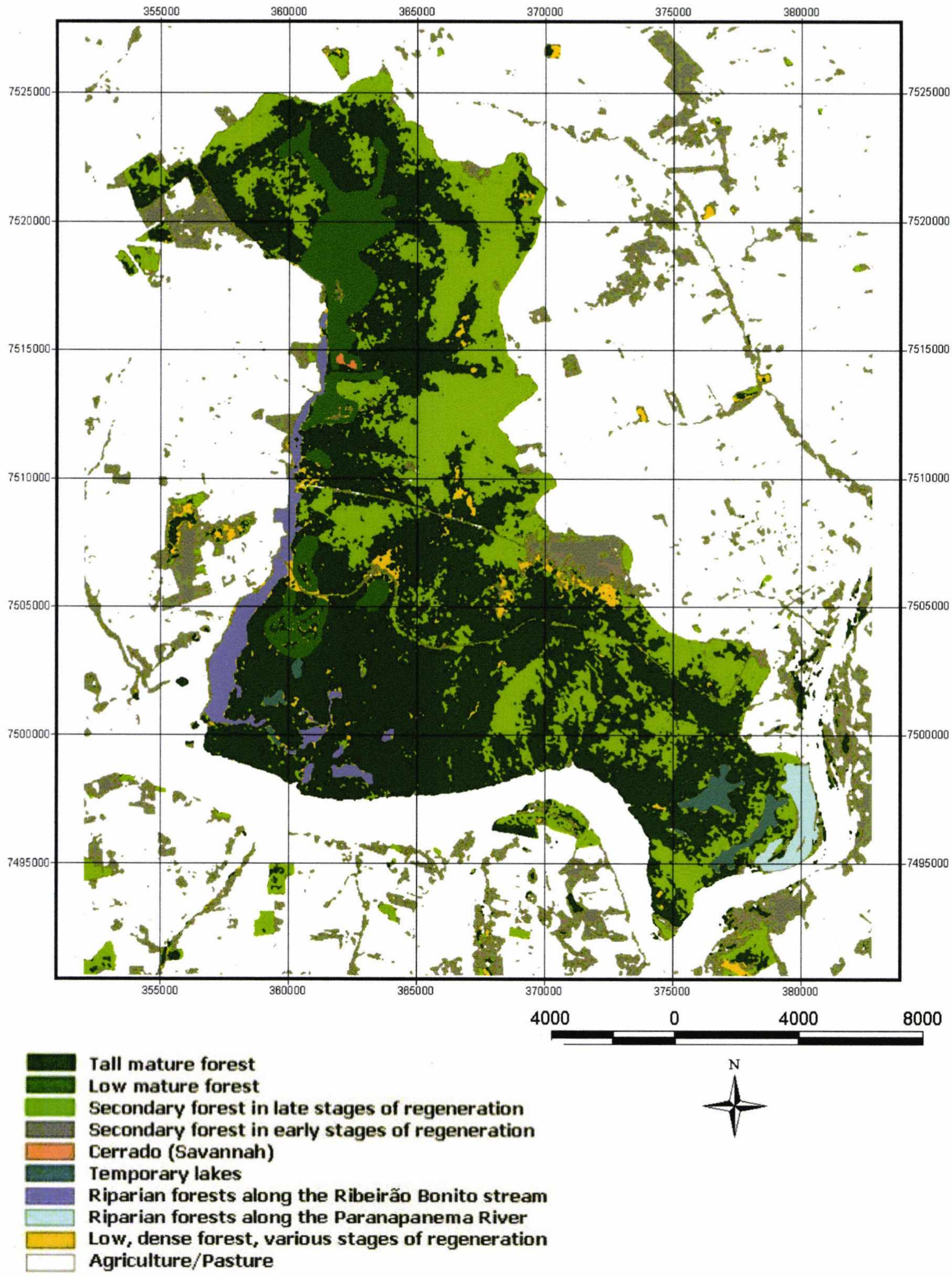


Figure 2.7. Map of habitat types found in Morro do Diabo State Park, São Paulo, Brazil, and surrounding buffer zone. Extracted from the Morro do Diabo State Park Management Plan (Faria & Pires 2006). Figures 2.5 and 2.6 provide further reference on the location of Morro do Diabo State Park.

2.6 General Methods

2.6.1 Logistics and Personnel

This 12-year lowland tapir study in Morro do Diabo was based at the field station of IPÊ - Instituto de Pesquisas Ecológicas (Institute for Ecological Research) in the Municipality of Teodoro Sampaio, São Paulo State, Brazil. IPÊ is a non-governmental-organisation (NGO) founded in 1992, in São Paulo, Brazil. While most of IPÊ's projects and initiatives are carried out in the Atlantic Forests of São Paulo and Paraná States, the organisation is also very active in other regions and biomes of Brazil, including the Amazon and, more recently, the Pantanal. Today, IPÊ works with a small core of approximately 100 professionals. IPÊ's work focuses on five main conservation programmes: (i) Wildlife Research, Conservation and Management; (ii) Wildlife Medicine; (iii) Environmental Education; (iv) Landscape Restoration; and, (v) Training and Capacity-Building. As a founding member of IPÊ, I have been working for the organisation as a research coordinator since January 1996.

The study area of Morro do Diabo is located at ~15 km from Teodoro Sampaio. Transportation to and from the field site as well as most field activities were carried out by car. The project owned two Volkswagen vehicles.

The field team included a multidisciplinary group of professionals that participated in, or were responsible for, different components of the study for varying lengths of time. The team included biologists, forest engineers, wildlife veterinarians, and geneticists from a variety of institutional affiliations as well as local field assistants.

2.6.2 Field Methods

Radio-telemetry was selected as the most appropriate methodology to conduct long-term monitoring of tapirs at Morro do Diabo. VHF radio-telemetry was used to study tapir ranging behaviour, habitat use and selection, and activity patterns.

From July 1997 to July 2008, a total of 35 individual tapirs, comprising 20 females and 15 males, or 27 adults, 6 sub-adults, and 2 juveniles were captured, immobilised, and sampled for biological materials in four different sections of Morro do Diabo: (i) West Border (N=8 tapirs), (ii) Northwest Border (N=2), (iii) Southeast Border (N=7), and (iv) Centre (N=18). The capture methods used were: (i) iron box traps, (ii) pitfalls, (iii) anaesthetic dart shooting, and (iv) wooden corrals. Seven different anaesthetic protocols were developed and used during the study. Twenty-five of the 35 captured tapirs were radio-collared, and 19 of them (13 females and 6 males, or 15 adults and 4 sub-adults) were monitored from July 1997 to

December 2006. Fourteen of the radio-collared tapirs (11 females and 3 males, or 12 adults and 2 sub-adults) were radio-tracked for extended periods of time from 8-36 months, while five individuals (2 females and 3 males, or 3 adults and 2 sub-adults) were radio-tracked for short periods from 2-4 months.

Three methods were used to estimate tapir population density: (i) Radio-Telemetry, (ii) Nocturnal Line-Transect Sampling, and (iii) Footprint Identification Technique (FIT). Population Viability Analysis (PVA) was carried out through the use of VORTEX software.

2.6.3 Timeframe of Study

Field work was carried out from October 1996 to July 2008, comprising approximately 12 years of data collection. Appendix I provides the timeframe of different activities carried out during this study in Morro do Diabo, including fieldwork, data analysis and fundraising.

2.6.4 Research Permits

This study required and obtained annual research permits from the Forestry Institute of São Paulo State (permit to conduct research activities in Morro do Diabo State Park - Processo SECRETARIA DO MEIO AMBIENTE Number 40.624/97) and from the Brazilian Federal Agency for the Conservation of Nature and Natural Resources of the Brazilian Ministry of the Environment (IBAMA - Instituto Brasileiro de Meio Ambiente e Recursos Naturais Renováveis) (permit for tapir capture, chemical immobilisation and manipulation, including collection of biological samples for epidemiological and genetics studies - Processo IBAMA Number 02027.004507/97-84).

Chapter 3

Spatial Ecology and Intra-Specific Interactions

Photo by Jefferson Lima

3.1 Introduction

Understanding the ways in which animals organise themselves in space and time is critical for addressing broader questions of ecology, behaviour, and conservation. Most importantly, knowledge of the ways in which animal populations use space in fragmented landscapes is vital for the design of management strategies that can promote the persistence of these populations over the long-term. The information required to answer these ecological and socio-biological questions typically involves parameters of spatial ecology, most importantly home range size, as well as parameters of intra-specific interactions, such as home range overlap, spatial territoriality, and social organisation. Patterns of spatial ecology and intra-specific interactions may be tied directly to life-history parameters such as body size (McNab 1963), reproduction (Gregory *et al.* 1987), growth (Bronikowski 2000), resource acquisition (Luiselli 2006), and reflect the results of complex interactions between animals and the external environment (Forester *et al.* 2007).

Home range is the fundamental measure of the use of space and time by animals (White & Garrot 1990; Hemson *et al.* 2005), and has important consequences for ecological processes (Jetz *et al.* 2004). Home range is the normal area an animal uses over some specified period of time to carry out the activities of securing food, mating, and caring for young (Burt 1943). The description of home range is vital to determine habitat preferences (Aebischer *et al.* 1993), carrying capacities, and aspects of species-extinction susceptibility (Woodroffe & Ginsberg 2000; Brashares 2003). Home range is typically characterised with descriptors of its size, shape and structure (Kenward 2001). Estimates of home range size may be needed for management purposes, such as designing protected areas, and establishing corridors between isolated patches of habitat (Schoener 1968; Hulbert *et al.* 1996). Shape may be important for analysing how home ranges conform to the landscape when meeting resource and security requirements (Redpath 1995). Home range structure provides information about core areas of use and centres of activity used with different degrees of intensity according to habitat content, or in extent of home range overlap with neighbouring animals (Poullé *et al.* 1994).

Home ranges are the spatial expressions of the behaviours animals perform to survive and reproduce (Burt 1943). Because survival and reproduction are often food-limited, the abundance and predictability of food resources in time and space are likely important factors influencing spatial organisation. Therefore, food is often cited as an important limiting factor determining the size of an individual's home range (McLoughlin & Ferguson 2000). Animals move and establish their home ranges in response to energetic needs, or to build a memory map of patches of food resources, or in response to the distribution of resting sites (South 1999). In fact, optimal foraging theory assumes that animals have complete knowledge of the spatio-temporal distribution of resources within their home ranges, allowing predictions of the resource depletion level at which an animal should leave each food patch (Stephens & Krebs 1986). Such area-restricted space use behaviour has fundamental consequences for many ecological processes, such as the distribution and abundance of organisms and population regulation (Gautestad & Mysterud 2005; Wang & Grimm 2007), habitat selection (Rhodes *et al.* 2005), predator–prey dynamics (Lewis & Murray 1993), biological transport processes and community structure (Fagan *et al.* 2007), or spread of diseases (Kenkre *et al.* 2007). In addition, animals interact with their neighbours and other conspecifics in a variety of ways, ranging from the use of non-exclusive home ranges to defence of exclusive territories (Begon *et al.* 1990; Geffen *et al.* 1999). Home ranges of conspecifics often overlap, sometimes even extensively. The determination of extent of home range overlap provides indications of the degree of dynamic interactions between individuals (Macdonald *et al.* 1980; Kernohan *et al.* 2001), and therefore elucidates aspects of spatial territoriality and social organisation (Macdonald & Amlaner 1980; Wronski 2005). Previous studies have showed that tapir species exhibit home range overlap between neighbouring individuals (Foerster & Vaughan 2002; Ayala 2003; Noss *et al.* 2003).

Body size is a major determinant of parameters of spatial ecology, and particularly of home range size (McNab 1963). Home range size and body mass are positively correlated for most animal feeding styles and seasons (Mysterud *et al.* 2001). Therefore, large terrestrial mammals - such as tapirs - have larger home ranges and a greater absolute mobility than do small mammals (Eisenberg 1980). Thus, while the spatial requirements of tapirs vary with the carrying capacity of different habitats found within their distribution range (Eisenberg 1997; Medici *et al.* 2007a), they usually require considerably large home ranges (Williams 1978; Williams 1984; Foerster 1998; Herrera *et al.* 1999; Foerster & Vaughan 2002; Noss *et al.* 2003; Ayala 2003; Lizcano & Cavelier 2004; Tobler 2008; Abdul Ghani 2009; Naranjo 2009). In addition to large home range sizes, tapirs have complex home range structures, with multiple core areas of use (Tobler 2008) that are established according to the distribution of patches of preferred habitat types.

Tapirs are widely recognised as "landscape species", *i.e.* "species that occupy large home ranges often extending beyond protected area boundaries, that have a significant impact on the structure and functioning of natural ecosystems, and that require a diversity of ecosystem types" (Sanderson *et al.* 2002; Coppolillo *et al.* 2003). Landscape species are usually large-bodied and wide-ranging, have large habitat and nutritional requirements, have relatively low reproductive rates, and tend to occur naturally at low population densities (Sanderson *et al.* 2002), all of which represent the life-history characteristics of tapirs. As a typical landscape species, the density of lowland tapir populations tend to be as low as 0.3 tapirs km^{-2} in different regions and habitats where they occur (Cullen *et al.* 2000; Aquino *et al.* 2001; Aquino & Calle 2003; Haugaasen & Peres 2005; Desbiez 2009).

Tapir populations rarely attain a high local abundance and so are particularly susceptible to habitat loss and fragmentation. Small, isolated tapir populations show rapid decline or even go extinct when disturbed (Medici *et al.* 2007a). Wide-ranging species with large spatial requirements generally cannot find sufficient food and other vital resources to survive in small, isolated areas over the long-term (McNab 1963; Redford & Robinson 1991). Chiarello (1999) analysed the effects of the Atlantic Forest fragmentation on resident mammal communities in six forest patches of different sizes, and recorded the presence of tapirs in the large patches but not in the small ones. Likewise, a biome-wide tapir survey has been under way for the past four years, and preliminary assessments of lowland tapir status in the Brazilian Atlantic Forests of Bahia, Espírito Santo, Paraná, Rio de Janeiro, Rio Grande do Sul, Santa Catarina, and São Paulo states have shown that tapirs rarely survive in forests smaller than 20 km^2 without recourse to larger forest patches. While tapirs persist in some areas where habitat is reduced to small scattered fragments, they appear to need recourse to fragments larger than 5 km^2 in clusters that total at least 15 km^2. On the other hand, tapirs disappear completely in landscapes where all the forest fragments are smaller than 5 km^2, even when these smaller fragments constitute a large percentage of the landscape (Flesher 2007). However, lowland tapirs are adapted to diverse natural habitats and have the ability to traverse areas of low quality habitat, such as agricultural crops and pasture lands, and so should be fairly resistant to landscape changes as long as large tracts of forest remain (Flesher 2007). Nevertheless, given the additional intensive pressures of hunting, road-kill, forest fires among other threats, the existence of large forest fragments does not necessarily guarantee that tapirs will survive and persist over the long-term. There are several large forest fragments throughout the Atlantic Forest range where there should still be tapirs, but where they have been extirpated by hunting (Flesher 2007). The low rates of population growth, long generation time, slow reproductive rate, and delay in first reproduction are life-history characteristics that make tapirs particularly susceptible to overhunting (Bodmer *et al.* 1997). Cullen *et al.* (2000) compared the abundance of mammalian species in slightly and heavily hunted fragments of Atlantic Forest of the Interior, including Morro do Diabo as one of the slightly hunted sites, and observed that tapirs could not cope with persistent hunting and were extirpated from heavily hunted sites.

The Atlantic Forest of the Interior of the Pontal do Paranapanema Region is the perfect environment for the assessment of the long-term viability of tapir populations in fragmented landscapes. The description of the species requirements in terms of space should provide a measure of the tapir behavioural plasticity to human-induced fragmentation of habitat. The characterisation of the spatial ecology and intra-specific interactions of lowland tapirs in Morro do Diabo, one of the last significant remnants of the Atlantic Forest of the Interior, will provide critical information for the assessment of the ability of tapir populations to survive and persist in severely fragmented landscapes over the long-term. In addition, the process of destruction and fragmentation of the Atlantic Forest of the Interior of the Pontal do Paranapanema Region is relatively recent when compared to areas in the eastern part of the biome. The short period since fragmentation, equivalent to 5-6 tapir generations, most probably means that patterns of genetic structure are still in transition, and therefore genetic drift and inbreeding may not have been observed yet (Gonçalves da Silva 2007).

In this Chapter, I examine aspects of tapir ranging behaviour and spatial territoriality and provide insights into their spatial ecology and intra-specific interactions. Analysis of tapir home range size, home range structure, and seasonal home range in Morro do Diabo, as well as the description of tapir movements throughout the fragmented landscape of the Pontal do Paranapanema Region, allowed for the characterisation of tapir spatial ecology. Estimates of home range overlap and overlap of core areas of use were used to examine aspects of tapir territoriality and intra-specific interactions. This information was used to determine tapir spatial requirements and how these influence the long-term survival and persistence of tapir populations in the fragmented landscape of the Atlantic Forest. This chapter also provides an overview on the use and reliability of radio-telemetry for studying tapirs.

3.2 Methods

3.2.1 Radio-Telemetry

Radio-telemetry was selected as the most appropriate methodology to study the movements of lowland tapirs in Morro do Diabo. Tapirs are mostly solitary, nocturnal, secretive animals, a combination of factors that makes it very difficult to study them through direct observations. Radio-telemetry was first used for wildlife research studies during the 1960's and since then has revolutionised studies of the use of space by animals, providing a valuable tool to learn more about their respective life histories (Kenward 2001). Locations of radio-tagged animals can be collected systematically, free from the restrictions and bias that may be imposed on visual records by elusive behaviour or dense vegetation. When carefully applied, the resulting sets of locations provide a solid basis for estimating aspects of spatial ecology, including home range size and structure, seasonal home range, and population density; intra-specific interactions such as home range overlap, territoriality, and social behaviour; as well as habitat use and selection, activity patterns, predation, mortality and survivorship, migration timing and routes (Samuel & Fuller 1994; Rodgers *et al.* 1996; Kenward 2001).

Until 1995, only two previous studies by the same researcher had utilised radio-telemetry to gather information on tapirs, first on Malayan tapirs in Malaysia (Williams 1978; Williams 1979; Williams 1980; Williams & Pétrides 1980), and later on Baird's tapirs in Costa Rica (Williams 1984). Since then, other tapir researchers have employed this methodology, although only a few of them have successfully collected data over the long-term: (i) Lowland Tapir: Tarcísio Silva Jr. (1997, unpublished results) in Brazil; Herrera *et al.* (1999), Ayala (2002), Ayala (2003), and Noss *et al.* (2003) in Bolivia; Tobler (2008) in Peru; (ii) Baird's Tapir: Foerster (1998), Foerster & Vaughan (2002) in Costa Rica; (iii) Mountain Tapir: Downer (2003) in Ecuador; Lizcano & Cavelier (2004), Lizcano (2006) in Colombia; and, (iv) Malayan Tapir: Traeholt (2002), Abdul Ghani (2009) in Malaysia.

3.2.2 Capture Sites

Radio-telemetry was used in four different sections of Morro do Diabo including: West Border, Southeast Border, Northwest Border, and Centre (Figure 3.1). Initial capture efforts in 1997 focused on the western and south eastern borders of Morro do Diabo. An early objective of the study was to evaluate if tapirs left the boundaries of Morro do Diabo to feed on agricultural crops so causing human-tapir conflict, an issue recorded in other areas of Atlantic Forest where tapirs caused damage to sugar cane, manioc and coffee plantations. Tapirs have also been known to damage young corn and other grain crops (McCabe 1970). Therefore, I initially sought to capture and radio-collar tapirs in the border areas of Morro do Diabo where

I would have a better chance to investigate this aspect. Indeed, I placed pitfall traps outside the boundaries, in the middle of sugar cane plantations and areas of pasture land, on several occasions. In 2002, I started captures in the north western border, for the same reason. Starting in 2003, I directed our capture efforts to the centre of Morro do Diabo, away from the borders, where I found significant sign of tapirs. I also made sporadic attempts to bait and capture tapirs in some of the small forest fragments in the surroundings of Morro do Diabo. However, the capture process in these areas proved time-consuming and costly given the small number of tapirs in the fragments.

Figure 3.1. Lowland tapir capture sites within Morro do Diabo State Park, São Paulo, Brazil. Figures 2.5 and 2.6 (Chapter 2) provide further reference on the location of Morro do Diabo State Park.

3.2.3 Capture Methods

I organised our capture efforts into short-term capture rounds, which were scheduled according to the season of the year and availability of the team's veterinarians. Most of the capture rounds were held during the dry season (June/July/August) when weather conditions were more favourable. Capture rounds were carried out for periods from 2-4 weeks. From July 1997 to December 2002, nine capture rounds were carried out. From January 2003 to July 2004, I hired a full time wildlife veterinarian and therefore managed to keep our traps open on a constant basis. From July 2004 to July 2006, I did not conduct any captures as I focused on monitoring radio-collared individuals. From July 2006 to July 2008, I carried out four capture rounds for the single purpose of collecting biological samples for long-term genetics and epidemiological monitoring. During each capture round, different capture methods would be attempted simultaneously.

The capture methods used were: (i) iron box traps (N=1 capture), (ii) pitfalls (N=15), (iii) anaesthetic dart shooting, by foot or from platform, with CO_2 pistols and rifles (N=5), and (iv) wooden corrals (N=23). Iron box traps, pitfalls, and wooden corrals provided physical restraint of the tapirs before anaesthesia. In all cases, before the construction of the actual traps, areas frequently used by tapirs were identified, scouted and pre-baited with mineral salt. On some occasions, I tried other types of bait such as a native palm fruits (*Syagrus romanzoffiana*), mangos, guavas and bananas, but salt proved to be the most efficient bait in Morro do Diabo. The bait only serves as extra incentive to tapirs to return to that area on a repeated basis. Therefore, the bait stations must be placed in areas where tapirs would be expected to be travelling regardless of the bait. Depending on the density of the tapir population to be studied, this first step is not necessarily an easy one. Prior local knowledge of tapir behaviour and the study area usually helps the researcher focus in on areas of greater tapir traffic. Once tapirs were visiting a particular bait station on a regular basis I would make a decision about the most appropriate capture method for the area and build the trap or a platform high on a tree brunch for the case of anaesthetic dart shooting.

3.2.3.1 Iron Box Traps

Iron box traps were made of stainless iron and had the following measurements: 2 m long, 1.2 m wide and 1.5 m high (Figure 3.2.1). These traps were fairly small and there was not enough internal space for a trigger. Therefore, when using this method a team member was up on a tree waiting to close the trap (with the help of a rope tied to the trap's door) in the case a tapir went inside. The rest of the team would be nearby and in the case of a capture would be called on a walkie-talkie to come to the site as rapidly as possible. One individual tapir was captured in one of our box traps and it was immobilised inside the trap through the use of a blow-pipe and an anaesthetic dart (Telinject). Once the animal fell under the effect of the anaesthesia it was carried outside of the trap for the manipulation procedures and recovery. The main advantage of this method was that box traps were portable and could be moved to different capture locations according to our needs. The main disadvantage was that due to lack of internal trap space the team had to manipulate the tapir outside of the trap and had little control of the recovery process. Another disadvantage was having a team member up on a tree platform waiting to close the trap. In some cases, tapirs approaching the traps felt the presence of human beings and walked away.

3.2.3.2 Pitfalls

Pitfalls consisted of 2.3 m long, 1.5 m wide and 2.2 m deep holes in the ground covered with corrugated roofing tiles and camouflaged with forest debris (Figure 3.2.2). In my experience, pitfalls less than 2 m deep allowed tapirs to escape. Pitfalls were checked twice a day, at 05:30 h and 16:00 h. Nearly all tapirs captured in pitfalls were found early in the morning. In the event of a capture, the tapir was immobilised and manipulated inside the pitfall. Tapirs were immobilised through the use of a blow-pipe and anaesthetic darts (Telinject). Once the capture procedures where finished the veterinarian would inject the reversal agent and the team would monitor the recovery of the animal very closely. When the tapir had fully recovered from the anaesthesia a ramp was opened into one of the sides of the hole and the animal was free to exit the hole via the ramp. The main advantage of the pitfalls was that tapirs were manipulated inside the trap and the team had full control of the recovery and release processes. Another advantage of this method was that it did not require baiting. The biggest disadvantage of the pitfall traps was that once a tapir had been captured I could not use that same trap again. The trap had to be closed and another pitfall had to be built nearby. Other important disadvantages of the pitfall traps were the difficulty and cost of digging such large holes. Groups of 4-5 people would take ~5-6 hours to dig and camouflage a pitfall. Other animals captured in the pitfall traps were jaguar, white-lipped peccary, brocket deer, small rodents, frogs, and snakes.

3.2.3.3 Anaesthetic Dart Shooting

Anaesthetic dart shooting usually required the construction of a platform up on a tree where one or two members of the team would sit and wait for tapirs to come to the bait station under the platform (Figure 3.2.3). The rest of the team would be waiting nearby. Waiting hours would be usually from 17:00-02:00 h. In some cases, it was possible to dart tapirs from the ground. When shooting from a distance we used a CO_2 powered rifle (Pneu-Dart), and anaesthetic darts (1.5-inch barbed needles) equipped with telemetry transmitters (Pneu-Dart) to facilitate the process of following and locating darted tapirs. Once a tapir had been darted the team would wait for ~10 min and then radio-track the anaesthetised animal in order to locate it. Darted tapirs were usually found no farther than 200-300 m from the darting site. The main advantage of the darting method was that it was very practical as it did not require any major constructions, which meant that the selected capture site was fairly undisturbed. Low cost was another important advantage. The main disadvantage of this method relied on the fact that darted tapirs were not physically restrained. There are some inherent dangers in darting an animal that is not confined. If the animal becomes frightened from the dart impact, it can easily run, covering a lot of ground prior to the effect of the anaesthetic drugs. In addition, the physiologic effect of stress may delay anaesthetic induction or even prevent an animal from becoming sedated enough to stop moving (Hernández-Divers & Foerster 2001). Darting from tree platforms was the main capture method used in a long-term Baird's tapir study in Corcovado National Park, Costa Rica (Foerster & Vaughan 2002).

3.2.3.4 Wooden Corrals

The wooden corrals were large wooden enclosures 3.5 m long, 1.5 m wide and 2 m high (Figure 3.2.4). The pillars of the traps were wider than 10 cm and the wooden boards thicker than 2.5 cm. These traps were equipped with a trigger installed in the back of the trap and attached to the door, which closed automatically when a tapir stepped on the trigger. Corrals were checked twice a day, at 05:30 h and 16:00 h. In the event of a capture, the tapir was immobilised and manipulated inside the corral. Tapirs were immobilised through the use of a CO_2 powered pistol (Telinject) and anaesthetic darts (Telinject). Once the capture procedures were finished, the veterinarian would administer the reversal agent and the team would monitor the recovery of the animal very closely. Once the tapir had fully recovered from the anaesthesia the door of the corral was opened and the animal was free to exit the trap through the door. As for the pitfalls, the main advantage of the corrals was that we could manipulate tapirs inside the trap and had full control of the recovery and release processes. Another important advantage of this method was that despite the high initial effort and cost to construct the traps, many different individual tapirs from the same area could be captured in the same trap. This reduced capture costs per tapir over the long-term and maximised our chances to collect data about home range overlap and intra-specific interactions between neighbouring individuals. In three of our wooden corrals we captured several different individual tapirs: 4 tapirs were captured in the Taquara Ceva Caçador trap; 6 tapirs were captured in the Taquara Areião trap; and 8 tapirs were captured in the Taquara Córrego trap. In four occasions, known individual tapirs were recaptured in these corral traps. The only disadvantage of the wooden corrals was that we had to repair and renovate them on a regular basis. Some of our wooden corrals have been in use since January 2003. Wooden corrals were used during 2003 and 2004 and during four capture rounds from July 2006 to July 2008. Other animals captured in the corrals were white-lipped peccary, collared peccary, brocket deer, and agouti.

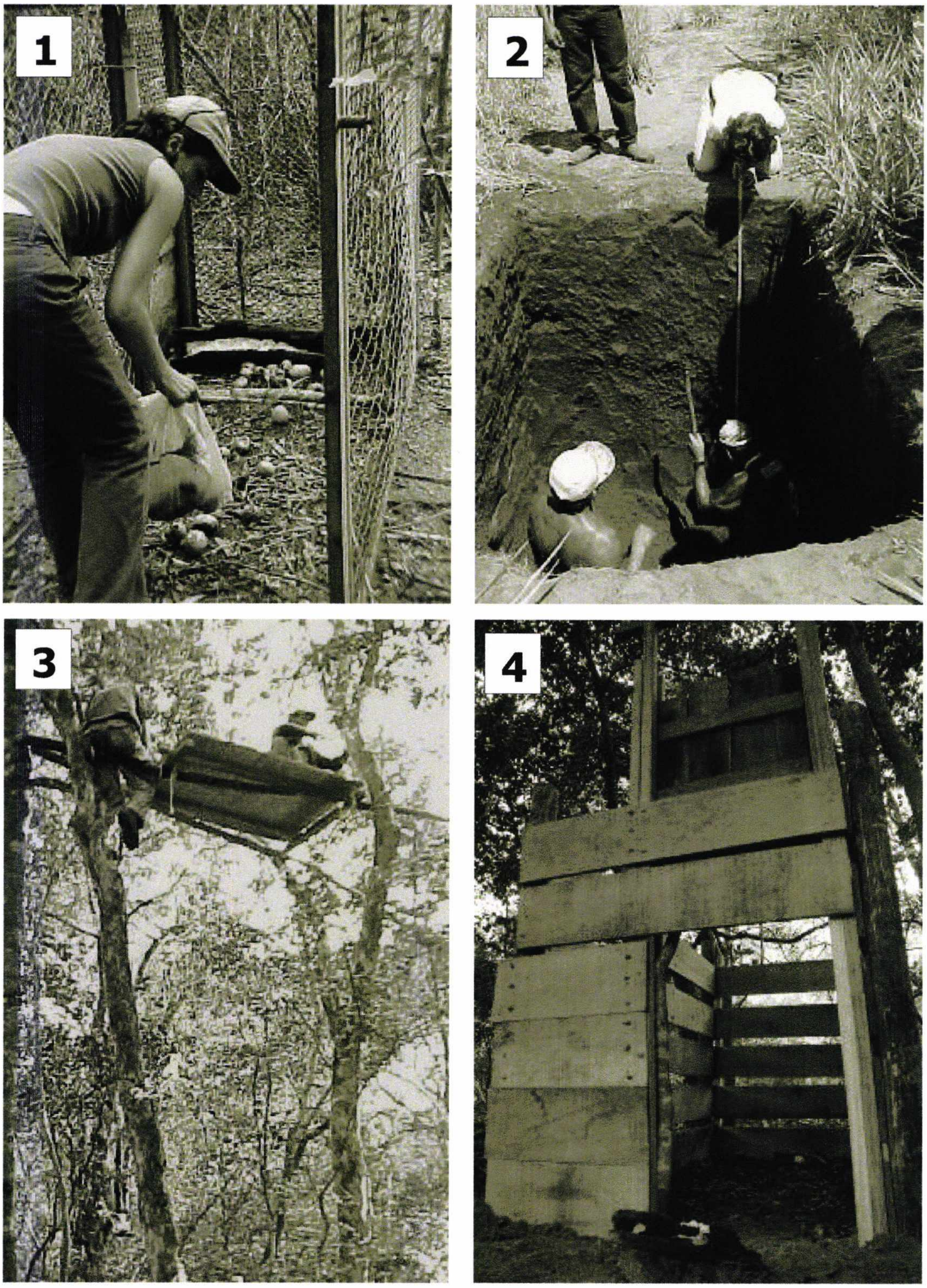


Figure 3.2. Capture methods used during the lowland tapir study in Morro do Diabo State Park, São Paulo, Brazil: 1- Iron box trap (N=1 captured tapir); 2- Pitfall trap (N=15); 3- Platform for anaesthetic darting (N=5); 4- Wooden corral (N=23). Photos by Patrícia Medici and Charles Foerster. Total number of tapir manipulations=44.

3.2.3.5 Trapping Effort and Trapping Success

Iron box traps were used in three capture rounds during the study. The trapping effort for this method was 165 24-hour periods of open traps. Forty-four pitfall traps were constructed during the study, 24 in the west border, 8 in the southeast border, 6 in the northwest border, and 6 in the centre. Eleven of them (25%) were successful in capturing tapirs. Pitfall traps were used in eight capture rounds, and the trapping effort was 1,230 24-hour periods of open traps. Anaesthetic dart shooting was attempted in 12 capture rounds and the trapping effort for this method was 260 nights (8 h/night). Nine wooden corrals were built during the study, two in the west border, two in the southeast border, and five in the centre of Morro do Diabo. Five of these traps were successful in capturing tapirs (55%). The trapping effort for this method was ~1,935 24-hour periods of open traps. Table 3.1 provides results of trapping success of each capture method.

Table 3.1. Trapping effort (hour), number of tapirs captured (N), and trapping success (tapirs/h) of the capture methods used in Morro do Diabo State Park, São Paulo, Brazil.

Capture Method	**Trapping Effort** (h)	**Tapir Captures** (N)	**Trapping Success** (tapirs/h)
Iron box traps	3,960	1	0.00025
Pitfalls	29,520	15	0.00050
Anaesthetic dart shooting	2,080	5	0.0024
Wooden corrals	46,440	23	0.00049

3.2.4 Chemical Immobilisation

Several anaesthetic protocols have been used previously for captive tapirs (Janssen *et al.* 1999; Nunes *et al.* 2001; Janssen 2003). However, anaesthetic protocols developed for captive animals may not be well-suited for the capture and immobilisation of free-ranging tapirs (Mangini & Medici 1998; Mangini *et al.* 2001a; Mangini *et al.* 2001b). Seven anaesthetic protocols based on a variety of anaesthetic agents were developed and tested by the project's veterinarians during this study. All protocols were based on combinations of Alpha-2-agonists with either dissociative drugs or opioid derivates. Two of the protocols were selected as the most appropriate for the chemical restraint of free-ranging lowland tapirs based on the following criteria: type of capture method, rapid induction and recovery, adequate immobilisation and muscle relaxation, reversibility, cost, and safety of the field team.

The first anaesthetic protocol selected was based on the association of Medetomidine Cloridrate (Domitor), Tiletamine/Zolazepan Cloridrate (Telazol), and Atropine. Atipemazole Cloridrate (Antisedan) was used as the antagonist to Medetomidine. This protocol was mostly used for dart shooting as it provided a short induction time (4-5 min), which is desirable for a capture method that does not provide physical restraint. The average manipulation time for this protocol was 130 min (N=9 manipulations; SD=53). The second protocol was based on a combination of Butorphanol (Torbugesic), Medetomidine, and Atropine. In some cases, Ketamine (Ketaset) was added to the protocol to extend the immobilisation. Naltrexone (Trexonil) was used as the antagonist to Butorphanol. Atipemazole was used as the antagonist to Medetomidine. This protocol was mostly used for situations where tapirs were physically restrained such as in pitfalls and wooden corrals. This protocol takes longer to take effect (11-12 min), but the anaesthesia occurs more smoothly as the animals attain a higher level of muscle relaxation. An important advantage of this protocol is that it is entirely and quickly reversible (1-2 min). The average manipulation time was 74 min (N=15 manipulations; SD=20). Atropine is not an anaesthetic agent. It was added to both anaesthetic protocols to inhibit excessive salivation and respiratory secretions as well as to reverse the blood pressure drop due to Alpha-2-agonists or dissociatives, which can potentially hamper the collection of blood samples. All of the anaesthetic and reversal agents used in both protocols have a large margin of safety for both humans and animals and have often been often recommended for Neotropical ungulates (Nunes *et al.* 2001). Anaesthetic and reversal doses were calculated using inter-specific allometric scaling based on estimated body weights of captured animals.

Anaesthetic agents were injected intramuscularly (IM) through the use of either a blow-pipe (Telinject), CO_2 powered pistol (Telinject) or rifle (Pneu-Dart), and anaesthetic disposable darts (Pneu-Dart). Reversal agents were injected intravenously (IV). The parameters of anaesthesia monitoring included heart rate and rhythm, rate of ventilations, rectal temperature, and oxygen saturation through pulse-oximetry (Table 3.2). Data on anaesthesia monitoring during immobilisations was continually evaluated and protocols adjusted accordingly in order to guarantee the well-being of the animals under anaesthesia, as well as the safety of the research team. Safety and emergency drugs used to improve respiratory and cardiac functions, such as Epinephrine, Atropine, Doxapran, Dopamine and oxygen supplementation, were available during manipulations.

Table 3.2. Parameters of anaesthesia monitoring obtained during 44 lowland tapir manipulations carried out in Morro do Diabo State Park, São Paulo, Brazil (N=number of manipulations; AV=average; SD=standard deviation; Max=maximum; Min=minimum).

Parameter of Anaesthesia Monitoring	**N**	**AV**	**SD**
Heart rate (Max)	18	80	19.0
Heart rate (Min)	18	67	16.6
Rate of ventilations (Max)	21	26	8.4
Rate of ventilations (Min)	21	19	8.0
Oxygen saturation % (Max)	17	95	3.8
Oxygen saturation % (Min)	17	80	18.9
Temperature ºC (Max)	9	36	0.8
Temperature ºC (Min)	9	36	0.8

3.2.5 Manipulation and Collection of Biological Samples

The first procedure carried out during tapir manipulations was the installation of the radio-collar. The transmitter package of the collar was placed right under the throat of the tapir. Collars were carefully fitted for the safety of the animals, sufficiently loose as to be comfortable and not interfere with swallowing or panting or any other regular activities of the animals. Initially, I attempted to ear tag tapirs (N=10) for visual identification by direct sightings, but without exception all ear tags fell off. Other procedures carried out during immobilisation included sexing, aging via tooth wear and appearance of foot cushions, corporal measurements, and collection of biological samples. The age estimations separated individuals into three different age classes including: juvenile (6 months to 1 year), sub-adult (1-4 years), and adult (over 4 years of age). Estimated weights and corporal measurements of tapirs captured in Morro do Diabo are presented in Chapter 2.

Biological samples were collected, adequately preserved and stored for genetics and epidemiological studies. Samples for genetics studies included blood (N=32 samples), skin biopsy tissues (N=23), faeces (N=4), and hair (N=13). Blood samples consisted of an average of 50 ml collected through venipuncture on the saphenous or jugular veins. The jugular vein is deep and not always easy to access. Biopsy samples consisted of 1cm^2 of skin collected from the tip of the ear. For the genetics assessment, fresh faecal samples were also systematically collected while walking trails in Morro do Diabo and surrounding forest fragments (N=170). Samples for genetics studies were analysed and DNA extracted at the EMBRAPA-CENARGEN laboratory in Brasília, Distrito Federal, Brazil. The results of genetics analysis carried out as a component of this study can be found in Gonçalves da Silva (2007).

Samples for health studies included blood (N=32 samples) for serology, haematology, blood chemistry, and blood parasites; swabs (N=20) for bacterial cultures (nasal, oral, ear, rectal, vaginal, urethra and preputial); urine (N=8) for urinalysis and sediment analysis; and ectoparasites (N=22) for identification. Samples were properly preserved and immediately transported or sent to reference laboratories for analysis. The serology analyses tested for 12 different types of infectious diseases relevant to tapirs and domestic livestock (cattle, horses and swine) in the Pontal do Paranapanema Region. Preliminary results of the epidemiological analyses were used for the Population Viability Analysis (PVA) modelling in Chapter 6. The complete results of epidemiological evaluation and long-term monitoring of tapir health in Morro do Diabo will be included in a Master's thesis currently under way.

Finally, during capture procedures I conducted a detailed evaluation of the general conditions of the tapirs inspecting for any visible external injuries, presence of scars, and ectoparasite load among others. For females, I inspected for any evidence of reproductive activity (lactating females, presence of vaginal secretions, superficial wounds caused by mounting). Four adult female tapirs were captured in their pre or post parturition period and it was possible to collect milk samples for bromatological and chemical analysis. All data collected during tapir manipulations was recorded through field data sheets, photographs and, in some occasions, videos.

Without exception, all captures and animal manipulations were carried out by one of the project's veterinarians. Veterinarians in the team were specialised in wildlife medicine and through this project have acquired many years of experience on the immobilisation and handling of free-ranging lowland tapirs. Capture stress and traumas are intrinsic risks of the handling of wild animals. However, well-planned capture procedures and the selection of a safe chemical restraint protocol can significantly reduce these risks. All our protocols for the capture, immobilisation and manipulation of tapirs, as well as for the collection, storage and analysis of tapir biological samples were reviewed and approved by the Veterinary Advisors of the Association of Zoos & Aquariums (AZA) Tapir Taxon Advisory Group (TAG), as well as the Veterinary and Genetics Committees of the IUCN/SSC Tapir Specialist Group (TSG). Further details about different tapir capture methods and anaesthetic protocols, as well as guidelines for the collection and storage of tapir biological samples can be found on the "Tapir Field Veterinary Manual" compiled and published by the Veterinary Committee of the IUCN/SSC Tapir Specialist Group (TSG) (Medici *et al.* 2007b). The Manual was largely based on results and experiences from this long-term lowland tapir study in Morro do Diabo.

3.2.6 Captured Individuals

From July 1997 to July 2008, a total of 35 different tapirs (20 females and 15 males, or 27 adults, 6 sub-adults, and 2 juveniles) were captured, immobilised through anaesthesia, manipulated and sampled for biological materials: (i) West Border (N=8; 5 females and 3 males, or 3 adults and 5 sub-adults), (ii) Northwest Border (N=2; 1 female and 1 male, or 2 adults), (iii) Southeast Border (N=7; 3 females and 4 males, or 7 adults), and (iv) Centre (N=18; 11 females and 7 males, or 15 adults, 1 sub-adult, and 2 juveniles).

Twenty-five of those 35 captured tapirs (13 females and 12 males, or 20 adults and 5 sub-adults) were radio-collared: (i) West Border (N=8 tapirs), (ii) Northwest Border (N=2), (iii) Southeast Border (N=6), and (iv) Centre (N=9). Six of the 25 radio-collared tapirs were not monitored because their collars fell off (N=5) or they died a few weeks after the capture (N=1). The individual that died was an adult male captured in June 2003 in the centre of Morro do Diabo. This male was very old and its teeth were almost completely worn down to the roots. It was severely thin and apparently very weak. I radio-collared the tapir in order to gather further information about its health conditions, but the animal was found dead 25 days after the capture. Ten of the 35 tapirs (7 females and 3 males, or 7 adults, 1 sub-adult, and 2 juveniles) were captured from July 2006 to July 2008 for the single purpose of collecting biological samples for a long-term genetics and epidemiological monitoring programme established in the later stages of the study. These individuals were not radio-collared.

Therefore, from July 1997 to December 2006, I radio-tracked a total of 19 tapirs (13 females and 6 males, or 15 adults and 4 sub-adults) for varying amounts of time: (i) West Border (N=7 tapirs), (ii) Northwest Border (N=2), (iii) Southeast Border (N=3), and (iv) Centre (N=7). Fourteen of the radio-collared tapirs (11 females and 3 males, or 12 adults and 2 sub-adults) were radio-tracked for extensive periods of time (8-36 months). Five of the radio-collared tapirs (2 females and 3 males, or 3 adults and 2 sub-adults) were radio-tracked for short periods of time (2-4 months) before their collars fell off (N=2) or stopped working (N=1), or before they were predated by either jaguar (N=1) or puma (N=1).

On two occasions, I captured adult females with offspring, the first time in a pitfall trap and the second time in a wooden corral. One calf was a male no older than 3-4 months of age, and the second was a female calf of ~5-6 months of age. These two calves were neither anaesthetised nor manipulated. The two juvenile tapirs captured during the study were immobilised and sampled for biological materials, but not radio-collared. Young tapirs gain weight and grow very fast; therefore placing collars on them may unnecessarily risk their lives.

I carried out nine tapir recaptures during the study for either collar retrieval (N=5) and/or collection of biological samples. Overall, during the study in Morro do Diabo I performed a total of 44 tapir immobilisations and manipulations. Appendix II provides complete information about each individual lowland tapir captured in Morro do Diabo State Park.

3.2.7 Telemetry Equipment

Very High Frequency (VHF) telemetry was used to study tapir movements in Morro do Diabo. The telemetry equipment was purchased from Telonics, a wildlife telemetry company based in Arizona, USA. The receiving system included a TR-4 VHF tracking receiver (150-164MHz) and a RA-14K VHF antenna (150-164MHz). The TR-4 receiver is small, lightweight, and designed for easy field use. The RA-14K antenna is a handheld directional "H" antenna made of flexible rubber. The antenna was connected to the receiver through a RW-2 coaxial cable.

The transmitter collar model was an adapted version of MOD-500 HCP (High Capacity Transmitter), which was designed and manufactured by Telonics especially for lowland tapirs based on several intrinsic characteristics of the species (Figures 3.3.1 and 3.3.2). These characteristics included size, weight, shape of the neck, presence of the sagittal crest and, most importantly, the fact that these animals are constantly in the water. The weight of the radio-collar was ~300 grams. All electronic components, including transmitter, batteries, sensors, and power sources were totally enclosed in a hermetically sealed metal housing (CAST-1 Protective Casting), which eliminated the possibility of moisture penetration into the package. The collar itself was 1-m long to allow for different neck perimeters and made of 10" urethane over 1/8" butyl layers. The transmitter's antenna was placed internally in between the layers of the collar to prevent it from breaking off. I requested Telonics to place metallic rivets all along the length of the collar, in both sides of the internal antenna, in order to prevent the layers from coming apart. The frequency of the transmitters was 164MHz. The batteries of the transmitters were made to last for 36 months. In the field, they lasted for an average of 30 months (minimum=18 months, maximum=36 months).

The transmitters were equipped with a MS6A Mortality-Motion Sensor programmed with a 1-minute delay. A motion-sensitive sensor switch detects animal movement and provides "active/alive" or "inactive/dead" pulse periods depending on the activity of the animal. The microprocessor continuously monitors the motion switch to determine when motion occurs. Once per second, the microprocessor increments an "activity counter" if motion was detected during the preceding 1-second time period. This "activity counter" keeps a running total of the number of times motion was detected over a user-defined mortality evaluation time (in the case of this study, 1 min). This adaptation of the mortality sensor allowed for the study of activity patterns of tapirs in Morro do Diabo.

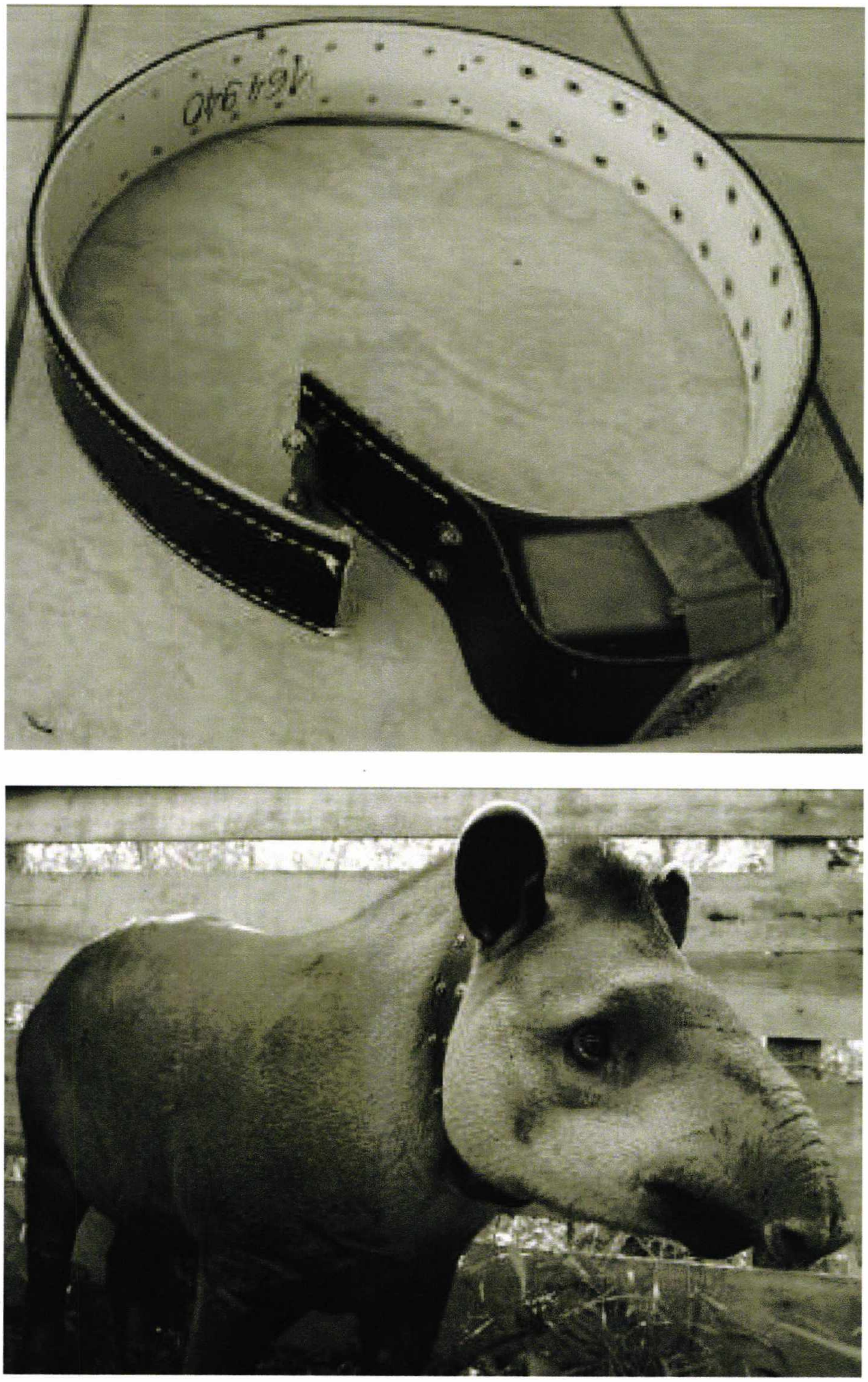


Figure 3.3. 1- Picture of radio-collar designed for the lowland tapir study in Morro do Diabo State Park, São Paulo, Brazil. Photo shows the metallic rivets placed along the length of the collar. 2- View of a radio-collar on a tapir. Photos by Patrícia Medici.

3.2.8 Telemetry Data Collection

I started radio-tracking tapirs immediately following their radio-collaring. After the capture, tapirs were continuously monitored for 72 h in order to ensure that the capture procedures had not affected them in any way. After this initial period, I continued to radio-track collared individuals following a pre-established sampling design.

Tapirs were radio-tracked on foot or by car, depending on terrain and weather conditions. Radio-collared tapirs were located by using the receiver and directional antenna to determine the direction of maximum signal strength and obtain a compass bearing (azimuth angle) to the target animal (transmitter). Coordinates of tapir locations were calculated by triangulation. Triangulation bearings were taken from two separate fixed stations along trails and roads inside and around Morro do Diabo. I established 162 fixed triangulation stations with known UTM locations (*Universal Transverse Mercator*) in four sections of Morro do Diabo. Triangulation stations were located at an average distance of 850 m from each other. Bearings were taken within 5 min of each other in order to maximise location accuracy. For each bearing, I recorded date, time, azimuth angle, and activity (active or inactive). The main problem with applying VHF telemetry in forest habitat is that the reach of the transmitter signal is usually less than 2 km, making it difficult to locate study animals. Therefore, I established the triangulation stations as I moved forward with data collection of each study tapir and as I learned more about their respective areas of use.

During the first five years of the study, I monitored each radio-collared tapir for 5 days per month, 24 hours a day. Each tapir was located every 30 minutes during the sampling period. This initial intensive sampling design generated ~240 locations per study animal per month, which allowed me to gather detailed data about tapir activity patterns. In the later four years of the study, I simplified the sampling design and concentrated data collection on crepuscular times, 3 hours at dawn (04:00-07:00 h) and 3 hours at dusk (17:00-20:00 h), for 2 days per month. Based on our preliminary data analysis and reviewed literature, these periods appeared to be the two main peaks of tapir activity. I continued to triangulate tapirs every 30 min. However, if a given tapir was inactive in the same location for long periods of time I would triangulate that particular location only once. With this sampling design I obtained ~24 locations per study animal per month. Appendix III provides detailed information about timeframes of monitoring of all 19 radio-tracked tapirs.

3.2.9 Telemetry Data Screening

The triangulation bearings obtained for each study animal were used to calculate the coordinates of tapir locations using the computer software TRACKER 1.1 (Camponotus Radio Location Systems AB 1994). The coordinates of tapir locations were then plotted on digitalised maps and satellite images of Morro do Diabo and surrounding forest fragments, and studied in a geo-referenced context produced by ArcGIS 9.X. software (ESRI-GIS Mapping Software, USA) and the Home Range Extension (HRE) for ArcView 3.3 (Hooge & Eichenlaub 2000).

Before the actual data analysis, I carried out a process of data screening and cleaned up the datasets of each one of the 19 radio-tracked tapirs. First, I removed all locations generated by triangulations where the difference between the two compass bearings was smaller than 30°. These triangulations generate intrinsic errors that can significantly alter the estimates of ranging behaviour parameters, particularly home range size. This is usually a result of human error (*i.e.* failure to determine the direction of maximum signal strength leading to a failure to obtain an accurate bearing), equipment failure (*i.e.* malfunctioning of receiver, antenna, or compass), presence of a water course near the triangulation station or in between the data collector and the target animal/transmitter (water causes signal reflection), presence of dense forest between the data collector and the target animal/transmitter, or a combination of two or more of these factors. Second, I removed all repeated locations obtained when an animal was inactive and in the same location for long periods of time. This usually occurred during the hottest periods of the day. Repeat locations can cause significant statistical dependence among data samples.

A total of 7,537 tapir locations were obtained during the study. After data screening, 3,103 of these or ~40% of the locations were omitted from the analysis. Most of the omitted locations (3,037) came from the datasets of 10 tapirs monitored during the initial intensive sampling in the first five years of the study. A total of 2,699 of these were repeated locations, and 338 generated large error ellipses. Only 66 locations were removed from the datasets of the nine tapirs monitored during the later four years of the study.

3.2.10 Tapir Spatial Ecology

3.2.10.1 Home Range Size

Home range size (km^2) for each of the 19 tapirs (13 females and 6 males, or 15 adults and 4 sub-adults) radio-tracked during the study in Morro do Diabo was calculated by using two different estimators: Kernel Density Estimator 95% (KDE95%) and Minimum Convex Polygon 95% (MCP95%). Mean home range size was calculated for all 19 tapirs, both sexes, and different age classes. KDE is widely viewed as the most reliable method of home range estimate in ecology (Powell 2000; Kernohan *et al.* 2001; Hemson *et al.* 2005). KDE has the advantage over MCP in that it not only outlines the outer home range boundary, but also describes the internal structure of the home range allowing for the identification of higher-usage areas within the home range, *i.e.* core areas of use and centres of activity (Hooge *et al.* 2001). KDE do not rely on outlying points to anchor their corners, and are less influenced by distant points, thereby excluding unused areas and leading to more accurate depictions of space use (Hemson *et al.* 2005). KDE and MCP results were compared, but MCP results were mostly reported to allow for comparisons with other lowland tapir studies. MCP was calculated using the Home Range Extension (HRE) for computer software ArcView 3.3 (Hooge & Eichenlaub 2000). KDE was calculated using ArcGIS 9.X (ESRI-GIS Mapping Software, USA). The most important input parameter to be defined when employing KDE estimates is the smoothing factor "h" (Silverman 1986). I used a Gaussian bivariate normal kernel and the Least Squares Cross-Validation (LSCV) method to estimate smoothing factor. LSCV is often recommended as the most appropriate technique for estimating "h" (Seaman & Powell 1996; Hemson *et al.* 2005). Data were rescaled for unit variance.

3.2.10.2 Maximum Distance Moved (MDM)

I used tapir home range results obtained through MCP95% to calculate the Maximum Distance Moved (MDM) for each one of the 19 tapirs radio-tracked in Morro do Diabo. Mean MDM was calculated for all 19 tapirs, both sexes, and different age classes. MDM was calculated using the Home Range Extension (HRE) for computer software ArcView 3.3 (Hooge & Eichenlaub 2000). Half MDM is generally used as a proxy of home range radius and gives a measure of home range structure.

3.2.10.3 Size of Core Areas of Use

The size of core areas of use (km^2) within the home ranges of each of the 19 tapirs radio-tracked in Morro do Diabo was calculated by using Kernel Density Estimator at both the KDE50% and KDE25% levels, using ArcGIS 9.X (ESRI-GIS Mapping Software, USA). Mean core area of use was calculated for all 19 tapirs, both sexes, and different age classes.

3.2.10.4 Seasonal Home Range

Seasonal home range (km^2) in dry and wet seasons for each of the 14 tapirs radio-tracked from 8-36 months was calculated by using Kernel Density Estimator (KDE95%), using ArcGIS 9.X (ESRI-GIS Mapping Software, USA). Mean seasonal home range in dry and wet seasons was calculated for all 14 tapirs, both sexes, and different age classes. In addition, I calculated core areas of use (KDE50% and KDE25%) in dry and wet seasons. Lastly, I calculated the overlap between the home ranges used in dry and wet seasons and examined the variation in location of seasonal home ranges.

3.2.10.5 Determination of Home Range Size over Time

I examined home range determination over time in two different ways. First, I calculated the overlap of annual areas of use between consecutive years of radio-tracking of the same tapir, and analysed the gradual increase in estimate of home range size over the years. The size of annual areas of use (KDE95%, km^2) and overlap between consecutive years (% and km^2) was calculated using ArcGIS 9X (ESRI-GIS Mapping Software, USA). For this analysis, I included 12 tapirs (10 females and 2 males, or 10 adults and 2 sub-adults) radio-tracked for over 18 months. Six of these tapirs were radio-tracked for periods from 18-24 months and so the increase in estimate of their home range size was analysed over a period of 2 years. The other six tapirs were radio-tracked for periods from 28-36 months, so the increase in estimate of their home range size was analysed over a period of 3 years.

Second, I plotted the cumulative size of monthly areas of use of six tapirs monitored for over 22 months, and determined the point in time or the number of locations required for their home ranges to reach an asymptote (Laver 2005). This allowed me to determine the minimum number of months of radio-tracking, as well as the minimum number of locations needed, to determine the full extent of the home range size for lowland tapirs. Home range analysis should be estimated using data that encompass the full range of variation in movement behaviour attributable to sex and age differences (Harris *et al.* 1990). To ensure that the sampling duration covers the full range of behaviours exhibited by the study species, it is necessary to calculate asymptotes.

3.2.11 Tapir Intra-Specific Interactions

3.2.11.1 Home Range Overlap

Home range overlap between neighbouring tapirs was calculated by Kernel Density Estimator (KDE95%) using ArcGIS 9.X (ESRI-GIS Mapping Software, USA). I calculated both percentage and area of overlap (km^2). Initial calculations of home range overlap were carried out for all possible combinations of pairs of individual tapirs radio-tracked concurrently. I then obtained mean values of home range overlap between the sexes (female-female, female-male, male-male), and between age classes (adult-adult, sub-adult-sub-adult, adult-sub-adult), as well as general mean values of tapir home range overlap for the study area.

3.2.11.2 Overlap of Core Areas of Use

Overlap of core areas of use between neighbouring tapirs was calculated by Kernel Density Estimator at both the KDE50% and KDE25% levels using ArcGIS 9.X (ESRI-GIS Mapping Software, USA). I calculated both percentage and area (km^2) of core area overlap. Initial calculations of 50% and 25% core area overlap were carried out for all possible combinations of pairs of tapirs radio-tracked concurrently. I then obtained mean values of core area overlap between the sexes (female-female, female-male, male-male), and between age classes (adult-adult, sub-adult-sub-adult, adult-sub-adult), as well as general mean values of tapir 50% and 25% core area overlap for the study area. Results of home range overlap and overlap of core areas of use were used to make inferences about the social organisation of tapirs in Morro do Diabo.

3.2.12 Statistical Significance

When appropriate, I compared results for differences in ranging parameters using Student's t-test, Mann-Whitney Rank Sum Test and One-Way Analysis of Variance (ANOVA). For these analyses I used the Sigma Stat 3.1 software package.

3.3 Results

3.3.1 Tapir Spatial Ecology

3.3.1.1 Home Range Size

Individual home range size varied widely among the 19 tapirs radio-tracked during the study in Morro do Diabo, including 14 tapirs radio-tracked from 8-36 months (long-term) and 5 tapirs radio-tracked from 2-4 months (short-term) (Table 3.3). The home range size varied from 1.1-14.2 km² when estimated using Kernel Density Estimator (KDE95%), with an average of 4.9 km². The home range size varied from 1-13.2 km² when estimated using Minimum Convex Polygon (MCP95%), with an average of 4.1 km² (Tables 3.3 and 3.4). There was no difference between home range size obtained by KDE95% and MCP95% (T=353.000; N=19-19; P=0.620).

The mean home range size for females was 4.7 km² when using KDE95%, and 3.8 km² when using MCP95%. The mean home range size for males was 5.4 km² when using KDE95%, and 4.7 km² when using MCP95% (Table 3.4). There were no differences in home range size between the sexes, either when estimated using KDE95% (T=69.000; N=6-13; P=0.456) or MCP95% (T=62.000; N=6-13; P=0.895).

The mean home range size for adults was 3.9 km² when using KDE95%, and 3.7 km² when using MCP95%. The mean home range size for sub-adults was 8.5 km² when using KDE95%, and 5.7 km² when using MCP95% (Table 3.4). There were no differences in home range size between different age classes, either when estimated using KDE95% (t=-2.398; DF=17; P=0.028) or MCP95% (T=54.000; N=4-15; P=0.177).

When running the same analyses for a second group of tapirs that only included the 14 tapirs radio-tracked from 8-36 months, results were very similar. I was interested to determine if removing the animals monitored in the short-term from the dataset would affect final results. While the home range curves of most individuals monitored in the long-term reached asymptotes over time, the home ranges of the five tapirs radio-tracked for short periods of time did not reach an asymptote.

For the second group, the mean home range size was 4.7 km² when estimated using KDE95%, and 4.4 km² when estimated using MCP95% (Table 3.4, Group 2). The mean home range size for females was 5.0 km² when using KDE95%, and 3.8 km² when using MCP95%. The mean home range size for males was 3.6 km² when using KDE95%, and 6.5 km² when using MCP95% (Table 3.4, Group 2). There was no difference in home range size between the sexes, either when estimated using KDE95% (t=-0.529; DF=12; P=0.607) or MCP95% (T=26.000; N=3-11; P=0.640). The mean home range size for adults was 3.3 km^2 when using KDE95%, and 3.7 km^2 when using MCP95%. The mean home range size for sub-adults was 12.7 km^2 when using KDE95%, and 8.1 km^2 when using MCP95% (Table 3.4, Group 2). There was no difference in home range size between different age classes, either when estimated using KDE95% (t=-6.800; DF=12; P=<0.001) or MCP95% (T=23.000; N=2-12; P=0.171).

Table 3.3. Home range size (KDE95% and MCP95%, km²) of 19 lowland tapirs radio-tracked in four different sections (West Border, Southeast Border, Northwest Border, and Centre) of Morro do Diabo State Park (MDSP), São Paulo, Brazil. Fourteen tapirs were radio-tracked from 8-36 months (long-term, G2=Group 2). Five tapirs were radio-tracked from 2-4 months (short-term). The number of telemetry locations and number of months of radio-tracking are shown for each tapir. (*Minimum; **Maximum)

Individual	**Sex**	**Age Class**	**Area MDSP**	**KDE95%** (km²)	**MCP95%** (km²)	**Telemetry Locations** (number)	**Period of Radio-Tracking** (months)	**Timeframe of Radio-Tracking**
JOANA	Female	Adult	West Border	4.4	6.2	903	36	Long-term, G2
PAULETE	Female	Adult	West Border	4.2	6.3	439	33	Long-term, G2
CHU-CHU	Female	Sub-Adult	West Border	**14.2****	10.7	294	35	Long-term, G2
PATRICIA	Female	Sub-Adult	West Border	11.2	5.5	184	30	Long-term, G2
DOCINHO	Female	Adult	Southeast Border	3.1	1.9	74	22	Long-term, G2
JAMES BOND	Male	Adult	Southeast Border	1.9	1.5	292	29	Long-term, G2
GEORGETE	Female	Adult	Southeast Border	2.0	**1.0***	205	25	Long-term, G2
CHICO	Male	Adult	Centre	5.2	**13.2****	440	28	Long-term, G2
JULIA	Female	Adult	Centre	7.4	2.3	60	12	Long-term, G2
CIDAO	Male	Adult	Centre	3.8	4.8	28	8	Long-term, G2
TONHA	Female	Adult	Centre	3.1	2.2	535	33	Long-term, G2
TINA	Female	Adult	Centre	2.0	2.1	451	27	Long-term, G2
MAMA	Female	Adult	Centre	1.9	1.6	234	18	Long-term, G2
ESPERTA	Female	Adult	Northwest Border	**1.1***	1.5	105	22	Long-term, G2
LUIZINHO	Male	Sub-Adult	West Border	4.6	3.4	37	3	Short-term
XUXA	Female	Adult	West Border	5.1	4.9	71	3	Short-term
JOAO	Male	Sub-Adult	West Border	4.1	3.2	26	2	Short-term
BABY	Female	Adult	Centre	1.5	3.5	40	4	Short-term
DEDINHO	Male	Adult	Northwest Border	12.7	2.0	10	2	Short-term

Table 3.4. Mean home range size (KDE95% and MCP95%, km^2) of lowland tapirs in Morro do Diabo State Park (MDSP), São Paulo, Brazil. Results for all 19 tapirs, Group 2 (14 tapirs radio-tracked from 8-36 months), both sexes, and different age classes are shown. (N=number of tapirs; SD=standard deviation; Min=Minimum; Max=Maximum)

	19 tapirs		**Group 2 (14 tapirs)**	
	KDE95% (km^2)	**MCP95%** (km^2)	**KDE95%** (km^2)	**MCP95%** (km^2)
ALL INDIVIDUALS	**4.9** (N=19; SD=3.8) Min 1.1 / Max 14.2	**4.1** (N=19; SD=3.2) Min 1.0 / Max 13.2	**4.7** (N=14; SD=3.8) Min 1.1 / Max 14.2	**4.4** (N=14; SD=3.7) Min 1.0 / Max 13.2
FEMALES	**4.7** (N=13; SD=4.0) Min 1.1 / Max 14.2	**3.84** (N=13; SD=2.8) Min 1.0 / Max 10.7	**5.0** (N=11; SD=4.2) Min 1.1 / Max 14.2	**3.8** (N=11; SD=3.0) Min 1.0 / Max 10.7
MALES	**5.4** (N=6; SD=3.7) Min 1.9 / Max 12.7	**4.7** (N=6; SD=4.3) Min 1.5 / Max 13.2	**3.6** (N=3; SD=1.6) Min 1.9 / Max 5.2	**6.5** (N=3; SD=6.0) Min 1.5 / Max 13.2
ADULTS	**3.9** (N=15; SD=3.0) Min 1.1 / Max 12.7	**3.7** (N=15; SD=3.2) Min 1.0 / Max 13.2	**3.3** (N=12; SD=1.8) Min 1.1 / Max 7.4	**3.7** (N=12; SD=3.5) Min 1.0 / Max 13.2
Adult Females	3.2 (N=11; SD=1.9) Min 1.1 / Max 7.4	3.1 (N=11; SD=1.9) Min 1.0 / Max 6.3	3.2 (N=9; SD=1.9) Min 1.1 / Max 7.4	2.8 (N=9; SD=2.0) Min 1.0 / Max 6.3
Adult Males	5.9 (N=4; SD=4.7) Min 1.9 / Max 12.7	5.4 (N=4; SD=5.4) Min 1.5 / Max 13.2	3.6 (N=3; SD=1.6) Min 1.9 / Max 5.2	6.5 (N=3; SD=6.0) Min 1.5 / Max 13.2
SUB-ADULTS	**8.5** (N=4; SD=5.0) Min 4.1 / Max 14.2	**5.7** (N=4; SD=3.5) Min 3.2 / Max 10.7	**12.7** (N=2; SD=2.1) Min 11.2 / Max 14.2	**8.1** (N=2; SD=3.7) Min 5.5 / Max 10.7
Sub-Adult Females	12.7 (N=2; SD=2.1) Min 11.2 / Max 14.2	8.1 (N=2; SD=3.7) Min 5.5 / Max 10.7	12.7 (N=2; SD=2.1) Min 11.2 / Max 14.2	8.1 (N=2; SD=3.7) Min 5.5 / Max 10.7
Sub-Adult Males	4.3 (N=2; SD=0.3) Min 4.1 / Max 4.6	3.3 (N=2; SD=0.2) Min 3.2 / Max 3.4	0 (N=0)	0 (N=0)

3.3.1.2 Maximum Distance Moved (MDM)

The Maximum Distance Moved (MDM) within the home ranges calculated for each of the 19 tapirs radio-tracked in Morro do Diabo varied from 1,595-6,112 m (Table 3.5). The mean MDM was 3,233 m. The mean MDM for females was 3,032 m and for males 3,667 m. The mean MDM for adult tapirs was 2,949 m and for sub-adults 4,294 m. There were no differences in MDM between the sexes (t=-0.939; DF=17; P=0.361), nor between different age classes (t=-1.867; DF=17; P=0.079).

Table 3.5. Maximum Distance Moved (m) by 19 lowland tapirs radio-tracked in four different sections (West Border, Southeast Border, Northwest Border, and Centre) of Morro do Diabo State Park (MDSP), São Paulo, Brazil. The home range size (MCP95%, km^2), number of locations, and number of months of radio-tracking are shown for each tapir. Mean MDM for all tapirs, both sexes, and different age classes are provided. (N=number of tapirs; *Minimum; **Maximum).

Individual	**Sex**	**Age Class**	**Area MDSP**	**MCP95%** (km^2)	**MDM** (m)	**Telemetry Locations** (number)	**Period of Radio-Tracking** (months)	**Timeframe of Radio-Tracking**
JOANA	Female	Adult	West Border	6.2	3,314	903	36	Long-term
PAULETE	Female	Adult	West Border	6.3	3,226	439	33	Long-term
CHU-CHU	Female	Sub-Adult	West Border	10.7	**6,112****	294	35	Long-term
PATRICIA	Female	Sub-Adult	West Border	5.5	3,818	184	30	Long-term
DOCINHO	Female	Adult	Southeast Border	1.9	2,135	74	22	Long-term
JAMES BOND	Male	Adult	Southeast Border	1.5	1,691	292	29	Long-term
GEORGETE	Female	Adult	Southeast Border	1.0	1,613	205	25	Long-term
CHICO	Male	Adult	Centre	13.2	5,740	440	28	Long-term
JULIA	Female	Adult	Centre	2.3	3,496	60	12	Long-term
CIDAO	Male	Adult	Centre	4.8	5,010	28	8	Long-term
TONHA	Female	Adult	Centre	2.2	2,704	535	33	Long-term
TINA	Female	Adult	Centre	2.1	1,807	451	27	Long-term
MAMA	Female	Adult	Centre	1.6	**1,595***	234	18	Long-term
ESPERTA	Female	Adult	Northwest Border	1.5	2,196	105	22	Long-term
LUIZINHO	Male	Sub-Adult	West Border	3.4	3,017	37	3	Short-term
XUXA	Female	Adult	West Border	4.9	4,346	71	3	Short-term
JOAO	Male	Sub-Adult	West Border	3.2	4,231	26	2	Short-term
BABY	Female	Adult	Centre	3.5	3,055	40	4	Short-term
DEDINHO	Male	Adult	Northwest Border	2.0	2,314	10	2	Short-term
Mean MDM (N=19)					**3,233**			
Mean MDM Females (N=13)					**3,032**			
Mean MDM Males (N=6)					**3,667**			
Mean MDM Adults (N=15)					**2,949**			
Mean MDM Sub-Adults (N=4)					**4,294**			

3.3.1.3 Size of Core Areas of Use

The size of core areas of use varied widely among the 19 tapirs radio-tracked in Morro do Diabo (Table 3.6). Core areas of use varied from 0.1-2.5 km^2 when estimated using KDE50%, with an average of 0.83 km^2. Core areas of use calculated at the 25% level varied from 0.03-0.9 km^2, with an average of 0.3 km^2 (Tables 3.6 and 3.7). The number of separate core units (kernels) within the home range of tapirs varied from 1-17 units at the 50% level, and from 1-9 units at the 25% level.

The mean core area of use for females was 0.8 km^2 at the 50% level, and 0.3 km^2 at the 25% level. For males, the mean core area of use at the 50% level was 0.9 km^2, and 0.3 km^2 at the 25% level (Table 3.7). There were no differences in size of core areas of use between the sexes, either at the 50% (T=72.000; N=6-13; P=0.313) or 25% level (T=71.000; N=6-13; P=0.357).

The mean core area of use for adults was 0.6 km^2 at the 50% level, and 0.2 km^2 at the 25% level. For sub-adults, the mean core area of use at the 50% level was 1.5 km^2, and 0.5 km^2 at the 25% level (Table 3.7). There was no difference in size of core areas of use between different age classes at the 50% level (T=60.000; N=4-15; P=0.051). However, sub-adult tapirs had significantly larger 25% core area of use than adults (T=61.000; N=4-15; P=0.040).

Table 3.6. Size of core areas of use (KDE50% and KDE25%, km^2) of 19 lowland tapirs radio-tracked in four different sections (West Border, Southeast Border, Northwest Border, and Centre) of Morro do Diabo State Park (MDSP), São Paulo, Brazil. Fourteen tapirs were radio-tracked from 8-36 months (long-term). Five tapirs were radio-tracked from 2-4 months (short-term). The home range size (KDE95%, km^2) is shown for each tapir. (*Minimum; **Maximum; Value in () is the number of separate core units within the home range of each tapir).

Individual	Sex	Age Class	Area MDSP	KDE95% (km^2)	KDE50% (km^2)	KDE25% (km^2)	Timeframe of Radio-Tracking
JOANA	Female	Adult	West Border	4.4	0.8 (17)	0.2 (9)	Long-term
PAULETE	Female	Adult	West Border	4.2	0.6 (10)	0.1 (4)	Long-term
CHU-CHU	Female	Sub-Adult	West Border	14.2	**2.5 (2)****	0.7 (1)	Long-term
PATRICIA	Female	Sub-Adult	West Border	11.2	2.4 (2)	**0.9 (2)****	Long-term
DOCINHO	Female	Adult	Southeast Border	3.1	0.4 (2)	0.2 (3)	Long-term
JAMES BOND	Male	Adult	Southeast Border	1.9	0.3 (2)	0.1 (3)	Long-term
GEORGETE	Female	Adult	Southeast Border	2.0	0.2 (1)	0.1 (1)	Long-term
CHICO	Male	Adult	Centre	5.2	0.8 (14)	0.2 (8)	Long-term
JULIA	Female	Adult	Centre	7.4	1.6 (2)	0.6 (1)	Long-term
CIDAO	Male	Adult	Centre	3.8	0.7 (4)	0.2 (4)	Long-term
TONHA	Female	Adult	Centre	3.1	0.3 (1)	0.1 (1)	Long-term
TINA	Female	Adult	Centre	2.0	0.4 (8)	0.1 (9)	Long-term
MAMA	Female	Adult	Centre	1.9	0.3 (9)	0.1 (6)	Long-term
ESPERTA	Female	Adult	Northwest Border	1.1	0.2 (11)	0.05 (5)	Long-term
LUIZINHO	Male	Sub-Adult	West Border	4.6	0.6 (2)	0.2 (1)	Short-term
XUXA	Female	Adult	West Border	5.1	0.4 (2)	0.2 (1)	Short-term
JOAO	Male	Sub-Adult	West Border	4.1	0.7 (4)	0.2 (2)	Short-term
DEDINHO	Male	Adult	Northwest Border	1.5	2.4 (1)	0.9 (1)	Short-term
BABY	Female	Adult	Centre	12.7	**0.1 (3)***	**0.03 (1)***	Short-term

Table 3.7. Mean core areas of use (KDE50% and KDE25%, km²) of lowland tapirs in Morro do Diabo State Park (MDSP), São Paulo, Brazil. Mean core areas of use for both sexes and different age classes are shown. (N=number of tapirs; SD=standard deviation; Min=Minimum; Max=Maximum).

	KDE50% (km²)	**KDE25%** (km²)
ALL INDIVIDUALS	**0.8** (N=19; SD=0.9) Min 0.1 / Max 2.5	**0.3** (N=19; SD=0.3) Min 0.03 / Max 0.9
FEMALES	**0.8** (N=13; SD=0.8) Min 0.1 / Max 2.5	**0.3** (N=13; SD=0.3) Min 0.03 / Max 0.9
MALES	**0.9** (N=6; SD=0.7) Min 0.3 / Max 2.4	**0.3** (N=6; SD=0.3) Min 0.1 / Max 0.9
ADULTS	**0.6** (N=15; SD=0.6) Min 0.1 / Max 2.4	**0.2** (N=15 ;SD=0.2) Min 0.03 / Max 0.9
Adult Females	0.5 (N=11; SD=0.4) Min 0.1 / Max 1.6	0.1 (N=11; SD=0.1) Min 0.03 / Max 0.6
Adult Males	1.0 (N=4; SD=0.9) Min 0.3 / Max 2.4	0.3 (N=4; SD=0.4) Min 0.1 / Max 0.9
SUB-ADULTS	**1.5** (N=4; SD=1.1) Min 0.6 / Max 2.5	**0.5** (N=4; SD=0.4) Min 0.2 / Max 0.9
Sub-Adult Females	2.5 (N=2; SD=0.02) Min 2.4 / Max 2.5	0.8 (N=2; SD=0.1) Min 0.7 / Max 0.9
Sub-Adult Males	0.6 (N=2; SD=0.1) Min 0.6 / Max 0.7	0.2 (N=2; SD=0.02) Min 0.2 / Max 0.2

3.3.1.4 Seasonal Home Range and Core Areas of Use

The wet season home range of tapirs was an average of 2.5 km^2, varied from 0.3-7.1 km^2. In the dry season, the home range of tapirs was an average of 2.6 km^2, varied from 0.4-16.7 km^2 (Table 3.8 and 3.9). There was no difference between tapir home range in wet and dry seasons (T=627.500; N=24-25; P=0.589). The overlap between tapir home range in wet and dry seasons varied from 19-98%, with an average of 69%.

There were no differences in size of seasonal home ranges between the sexes in either wet (t=-1.712; DF=22; P=0.101) or dry seasons (T=60.000; N=4-21; P=0.578). Likewise, there was no difference in size of seasonal home range between adult and sub-adult tapirs in the dry season (T=70.000; N=4-21; P=0.195). However, the wet season home range of sub-adult tapirs was significantly larger than adults (t=-2.472; DF=22; P=0.022).

The core area used by tapirs in the wet season was 0.4 km^2 at the 50% level, and 0.1 km^2 at the 25% level. The core areas used by tapirs in the dry season were exactly the same (Table 3.9). There were no differences between the core areas used by tapirs in wet and dry seasons either at the 50% (T=620.500; N=24-25; P=0.689) or 25% levels (T=620.000; N=24-25; P=0.697).

There were no differences in seasonal core areas of use at the 50% level between the sexes in either wet (t=-1.385; DF=22; P=0.180) or dry seasons (T=56.500; N=4-21; P=0.767). Likewise, there were no differences in seasonal core areas of use at the 25% level between the sexes tapirs in either wet (t=-1.201; DF=22; P=0.210) or dry seasons (T=52.500; N=4-21; P=1.000). There was no difference in seasonal core area of use at the 50% level between age classes in the dry season (T=71.000; N=4-21; P=0.170). However, the core area of use at the 50% level of sub-adult tapirs in the wet season was significantly larger than adults (t=-2.552; DF=22; P=0.018). Lastly, there were no differences in seasonal core area of use at the 25% level between age classes in either wet (T=68.000; N=4-18; P=0.067) or dry seasons (T=72.500; N=4-21; P=0.138).

Table 3.8. Home range (KDE95%, km^2) and core areas (KDE50% and KDE25%, km^2) in wet and dry seasons for 14 tapirs radio-tracked from 8-36 months in Morro do Diabo State Park (MDSP), São Paulo, Brazil. (F=female; M=male; A=adult; SA=sub-adult; *Minimum; **Maximum).

Individual Tapir (Age Class; Sex) Area MDSP	**Season/Year** (Wet/Dry-Year)	**Home Range**	**Core Area**	
		KDE95% (km^2)	**KDE50%** (km^2)	**KDE25%** (km^2)
JOANA (A;F) West Border	Wet Season-1997-1998	2.9	0.4	0.1
	Wet Season-1998-1999	2.5	0.5	0.1
	Wet Season-1999-2000	1.8	0.2	0.03
	Dry Season-1998	3.2	0.6	0.2
	Dry Season-1999	**0.4***	0.05	**0.01***
PAULETE (A;F) West Border	Wet Season-1998-1999	4.1	0.8	0.2
	Wet Season-1999-2000	0.5	**0.04***	**0.01***
	Dry Season-1998	2.6	0.5	0.1
	Dry Season-1999	3.4	0.7	0.3
	Dry Season-2000	0.5	**0.03***	**0.01***
CHU-CHU (SA;F) West Border	Wet Season-1998-1999	4.2	0.7	0.2
	Wet Season-1999-2000	5.1	1.2	**0.4****
	Wet Season-2000-2001	**7.1****	**1.2****	0.4
	Dry Season-1999	0.6	0.1	0.02
	Dry Season-2000	**16.7****	**2.3****	**0.7****
PATRICIA (SA;F) West Border	Wet Season-2000-2001	1.8	0.3	0.1
	Wet Season-2001-2002	3.0	0.4	0.1
	Dry Season-2001	2.8	0.5	0.2
	Dry Season-2002	6.5	1.6	0.6
DOCINHO (A;F) Southeast Border	Wet Season-1998-1999	0.9	0.2	0.1
	Dry Season-1998	3.1	0.5	0.2
	Dry Season-1999	1.4	0.3	0.1
JAMES BOND (A;M) Southeast Border	Wet Season-2001-2002	1.5	0.3	0.1
	Wet Season-2002-2003	2.4	0.3	0.1
	Dry Season-2001	0.7	0.1	0.03
	Dry Season-2002	1.8	0.2	0.05
GEORGETE (A;F) Southeast Border	Wet Season-2001-2002	1.0	0.2	0.04
	Dry Season-2001	2.2	0.3	0.1
	Dry Season-2002	0.8	0.1	0.1
CHICO (A;M) Centre	Wet Season-2003-2004	5.7	0.9	0.3
	Wet Season-2004-2005	6.3	1.0	0.3
	Dry Season-2004	3.2	0.6	0.2
JULIA (A;F) Centre	Wet Season-2003-2004	0.7	0.1	0.03
CIDAO (A;M) Centre	Dry Season-2004	3.4	0.6	0.2
TONHA (A;F) Centre	Wet Season-2004-2005	1.4	0.2	0.1
	Wet Season-2005-2006	0.6	0.1	0.04
	Dry Season-2004	1.5	0.3	0.1
	Dry Season-2005	0.8	0.1	0.04
	Dry Season-2006	1.2	0.2	0.1

TINA (A;F) Centre	Wet Season-2004-2005	2.1	0.4	0.1
	Wet Season-2005-2006	1.8	0.3	0.1
	Dry Season-2004	1.8	0.3	0.1
	Dry Season-2005	1.6	0.3	0.1
MAMA (A;F) Centre	Wet Season-2004-2005	1.9	0.2	0.1
	Dry Season-2004	1.8	0.3	0.1
	Dry Season-2005	1.6	0.3	0.1
ESPERTA (A;F) Northwest Border	Wet Season-2002-2003	1.2	0.2	0.1
	Wet Season-2003-2004	**0.3***	0.1	0.02
	Dry Season-2003	0.7	0.1	0.03

Table 3.9. Mean lowland tapir home range (KDE95%, km^2) and core areas of use (KDE50% and KDE25%, km^2) in wet and dry seasons in Morro do Diabo State Park (MDSP), São Paulo, Brazil. Mean seasonal home range size and core areas of use are shown for both sexes and different age classes. (N=number of wet/dry seasons considered for estimates; SD=standard deviation; Min=Minimum; Max=Maximum).

	Wet Season			**Dry Season**		
	KDE95% (km^2)	**KDE50%** (km^2)	**KDE25%** (km^2)	**KDE95%** (km^2)	**KDE50%** (km^2)	**KDE25%** (km^2)
ALL INDIVIDUALS	**2.5** N=48; SD=1.9 Min 0.3 Max 7.1	**0.4** N=48; SD=0.3 Min 0.04 Max 1.2	**0.1** N=48; SD=0.1 Min 0.01 Max 0.4	**2.6** N=50; SD=3.2 Min 0.4 Max 16.7	**0.4** N=50; SD=0.5 Min 0.03 Max 2.3	**0.1** N=50; SD=0.2 Min 0.01 Max 0.7
Females	**2.2** N=20; SD=1.7 Min 0.3 Max 7.1	**0.4** N=20; SD=0.3 Min 0.04 Max 1.2	**0.1** N=20; SD=0.1 Min 0.01 Max 0.4	**2.6** N=21; SD=3.5 Min 0.4 Max 16.7	**0.4** N=21; SD=0.5 Min 0.03 Max 2.3	**0.1** N=21; SD=0.2 Min 0.01 Max 0.7
Males	**4.0** N=4; SD=2.4 Min 1.5 Max 6.3	**0.6** N=4; SD=0.4 Min 0.3 Max 1.0	**0.2** N=4; SD=0.1 Min 0.1 Max 0.3	**2.3** N=4; SD=1.3 Min 0.7 Max 3.4	**0.4** N=4; SD=0.3 Min 0.1 Max 0.6	**0.1** N=4; SD=0.1 Min 0.03 Max 0.2
Adults	**2.1** N=19; SD=1.7 Min 0.3 Max 6.3	**0.3** N=19; SD=0.3 Min 0.04 Max 1.0	**0.1** N=19; SD=0.1 Min 0.01 Max 0.3	**1.8** N=21; SD=1.0 Min 0.4 Max 3.4	**0.3** N=21; SD=0.2 Min 0.03 Max 0.7	**0.1** N=21; SD=0.1 Min 0.01 Max 0.3
Sub-Adults	**4.2** N=5; SD=2.0 Min 1.8 Max 7.1	**0.7** N=5; SD=0.4 Min 0.3 Max 1.2	**0.2** N=5; SD=0.2 Min 0.1 Max 0.4	**6.6** N=4; SD=7.2 Min 0.6 Max 16.7	**1.1** N=4; SD=1.0 Min 0.1 Max 2.3	**0.4** N=4; SD=0.3 Min 0.02 Max 0.7

3.3.1.5 Determination of Home Range Size over Time

The annual areas of use calculated for 12 tapirs radio-tracked for over 18 months varied from 0.4-8.2 km^2, with an average of 2.5 km^2 (Tables 3.10 and 3.11). The home ranges of seven adult tapirs included in this analysis (Paulete, Tonha, Tina, Mama, James Bond, Georgete, and Esperta) reached an asymptote during the second year of data collection (Table 3.12). In contrast, the home ranges of the other five tapirs (3 adults: Joana, Chico, and Docinho; 2 sub-adults: Chu-Chu and Patrícia) only reached an asymptote during the third year of data collection.

In order to determine the minimum number of months of radio-tracking and the minimum number of locations needed to estimate the full extent of the home range size of tapirs, I plotted the cumulative size of monthly areas of use over time for six of the seven adult tapirs for which their home ranges reached asymptotes over periods of two years. The home ranges of these six tapirs reached asymptotes at an average of 16 months of radio-tracking (varied from 7-28 months) and 201 radio-telemetry locations (varied from 63-496) (Figure 3.4). When including the estimates of 36 months of radio-tracking of adult female Joana and adult male Chico in this analysis, the minimum number of months to reach an asymptote rises to 20 and the minimum number of locations rises to 319.

Table 3.10. Annual areas of use (KDE95%, km^2) of 12 tapirs radio-tracked for over 18 months in Morro do Diabo State Park, São Paulo, Brazil. The period of radio-tracking and number of locations are shown for each tapir. (F=female; M=male; A=adult; SA=sub-adult; *Minimum; **Maximum).

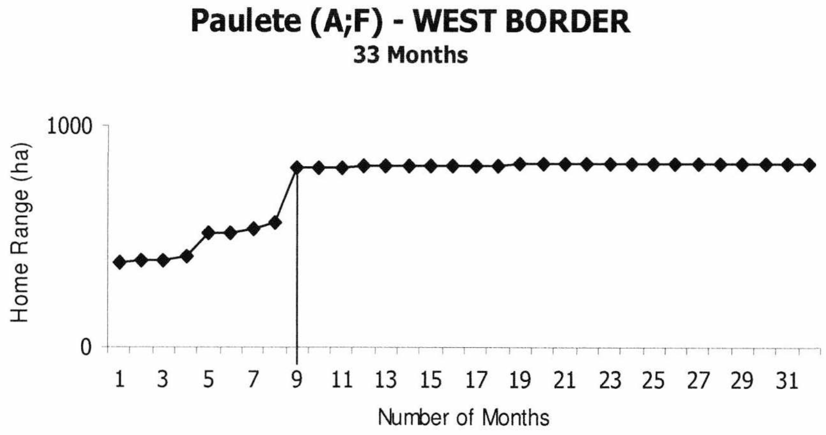
Individual Tapir (Age Class; Sex) (Period of data collection)	**Period** (month, year)	**Period of Radio-Tracking** (months)	**Telemetry Locations** (number)	**Annual Area KDE95%** (km^2)
JOANA (A;F) (36 months)	Jul1997-Jun1998	12	573	3.4
	Jul1998-Jun1999	12	249	2.2
	Jul1999-Jun2000	12	81	1.0
PAULETE (A;F) (33 months)	Feb1998-Jan1999	12	263	5.0
	Feb1999-Jan2000	12	112	2.3
CHU-CHU (SA;F) (35 months)	Aug1998-Jul1999	12	91	2.3
	Aug1999-Jul2000	12	101	**8.2****
	Aug2000-Jun2001	11	102	6.0
PATRICIA (SA;F) (30 months)	Aug2000-Jul2001	12	83	0.7
	Aug2001-Jul2002	12	59	3.1
CHICO (A;M) (28 months)	Jun2003-May2004	12	217	2.7
	Jun2004-May2005	12	119	4.3
TONHA (A;F) (33 months)	Apr2004-Mar2005	12	154	2.1
	Apr2005-Mar2006	12	253	0.9
TINA (A;F) (27 months)	May2004-Apr2005	12	118	3.5
	May2005-Apr2006	12	261	1.8
MAMA (A;F) (18 months)	May2004-Apr2005	12	130	2.1
DOCINHO (A;F) (22 months)	Feb1998-Jan1999	12	23	0.6
	Feb1999-Nov1999	10	51	3.1
JAMES BOND (A;M) (29 months)	Feb2001-Jan2002	12	111	1.0
	Feb2002-Jan2003	12	113	1.5
GEORGETE (A;F) (25 months)	Feb2001-Jan2002	12	109	2.2
	Feb2002-Jan2003	12	80	0.7
ESPERTA (A;F) (22 months)	Jun2002-May2003	12	44	1.0
	Jun2003-Feb2004	10	61	**0.4***

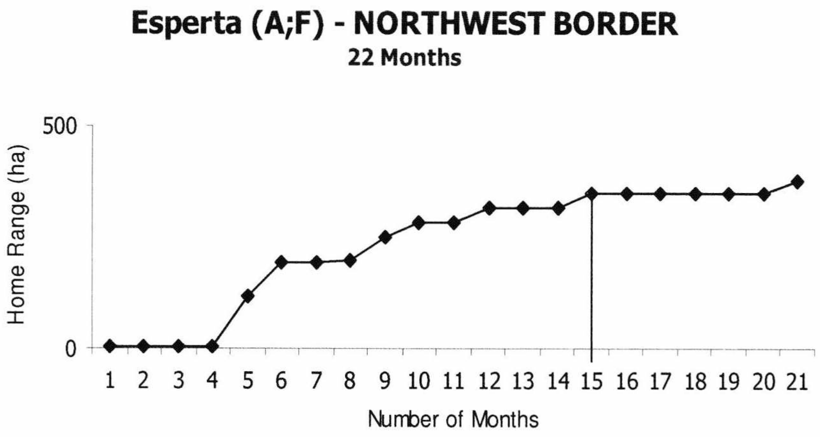
Table 3.11. Mean annual areas of use (KDE95%, km^2) of 12 tapirs radio-tracked for over 18 months in Morro do Diabo State Park, São Paulo, Brazil. Separate results for both sexes and different age classes are shown. (N=number of periods of 10-12 months considered as an annual sample; SD=standard deviation; Min=Minimum; Max=Maximum).

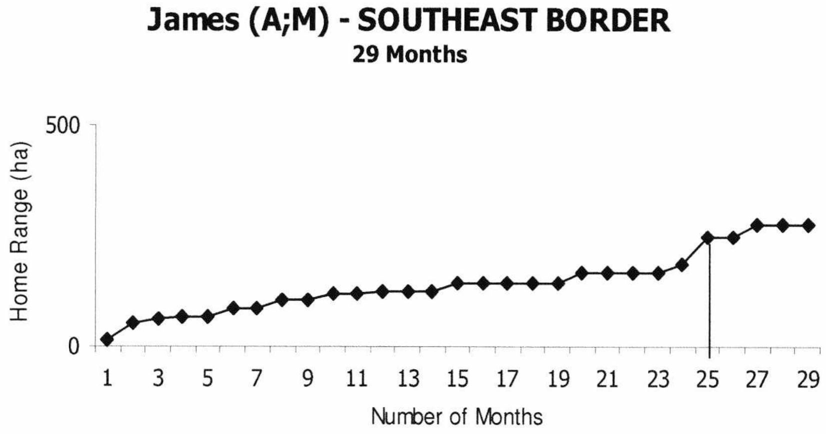
	Annual Area KDE95% (km^2)
ALL INDIVIDUALS	**2.5** (N=25; SD=1.9; Min 0.4; Max 8.2)
Females	**2.5** (N=21; SD=1.9; Min 0.4; Max 8.2)
Males	**2.4** (N=4; SD=1.5; Min 1.0; Max 4.3)
Adults	**2.1** (N=20; SD=1.3; Min 0.4; Max 5.0)
Sub-Adults	**4.1** (N=5; SD=3.0; Min 0.7; Max 8.2)

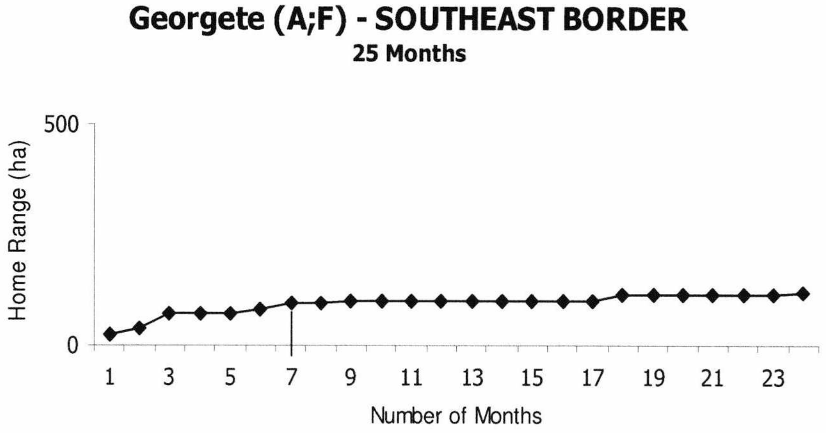
Table 3.12. Cumulative areas of use (KDE95%, km²) for consecutive years of radio-tracking of the same tapir, overlap of areas of use between consecutive years, and gradual increase in estimate of home range size over time for 12 tapirs radio-tracked in Morro do Diabo State Park, São Paulo, Brazil. (F=female; M=male; A=adult; SA=sub-adult; *Area of use in the 1st year; **Increase in HR estimate in the 2nd year; ***Increase in HR estimate in the 3rd year)

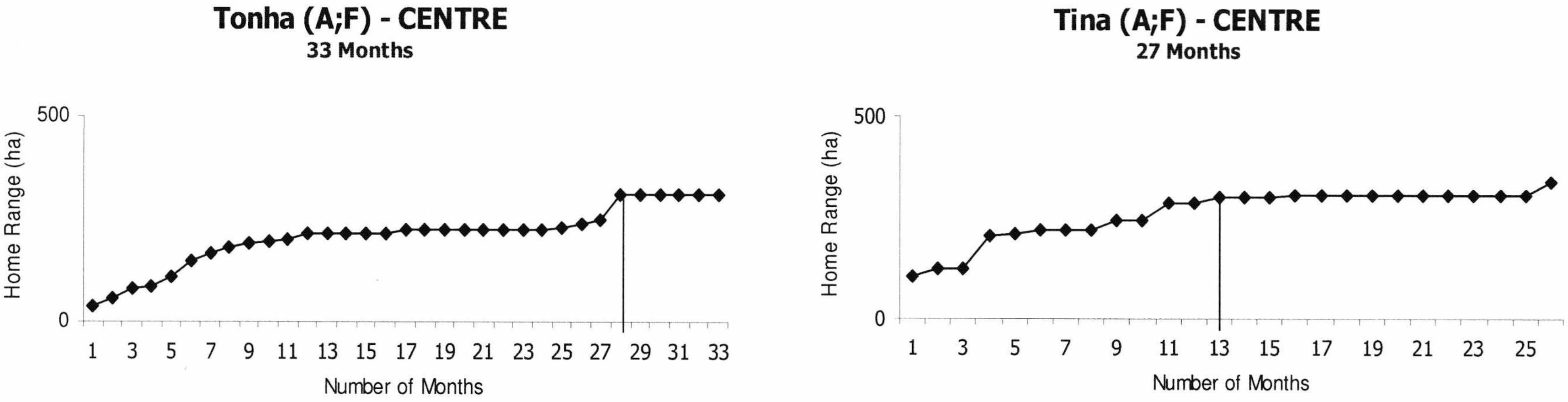
Individual Tapir (Age Class; Sex) (Period of data collection)	**Period** (month, year)	**Period of Radio-Tracking** (months)	**Cumulative Area of Use** (km²)	**Overlap** (km²)	**Increase in Estimate of Home Range Size** (km²)
JOANA (A;F) (36 months)	Jul1997-Jun1998	12	**3.4***	0.8	**1.3****
	Jul1998-Jun1999	12	2.2		
	Jul1997-Jun1999	24	4.7	0.7	**0.3*****
	Jul1999-Jun2000	12	1.0		
PAULETE (A;F) (33 months)	Feb1998-Jan1999	12	**5.0***	2.2	**0.1****
	Feb1999-Jan2000	12	2.3		
	Feb1998-Jan2000	24	5.2	0.6	**0.0*****
	Feb2000-Oct2000	9	0.6		
CHU-CHU (SA;F) (35 months)	Aug1998-Jul1999	12	**2.3***	1.9	**6.3****
	Aug1999-Jul2000	12	8.2		
	Aug1998-Jul2000	24	8.6	3.6	**2.4*****
	Aug2000-Jun2001	11	6.0		
PATRICIA (SA;F) (30 months)	Aug2000-Jul2001	12	**0.7***	0.4	**2.7****
	Aug2001-Jul2002	12	3.1		
	Aug2000-Jul2002	24	3.4	2.8	**3.0*****
	Aug2002-Jan2003	6	5.8		
CHICO (A;M) (28 months)	Jun2003-May2004	12	**2.7***	1.5	**2.8****
	Jun2004-May2005	12	4.3		
	Jun2003-May2005	24	5.4	2.5	**0.9*****
	Jun2005-Sep2005	4	3.4		
TONHA (A;F) (33 months)	Apr2004-Mar2005	12	**2.1***	0.8	**0.1****
	Apr2005-Mar2006	12	0.9		
	Apr2004-Mar2006	24	2.2	1.1	**0.1*****
	Apr2006-Dec2006	9	1.2		
TINA (A;F) (27 months)	May2004-Apr2005	12	**3.5***	1.7	**0.1****
	May2005-Apr2006	12	1.8		
MAMA (A;F) (18 months)	May2004-Apr2005	12	**2.1***	1.3	**0.2****
	May2005-Oct2005	6	1.5		
DOCINHO (A;F) (22 months)	Feb1998-Jan1999	12	**0.6***	0.5	**2.5****
	Feb1999-Nov1999	10	3.1		
JAMES BOND (A;M) (29 months)	Feb2001-Jan2002	12	**1.5***	0.9	**0.1****
	Feb2002-Jan2003	12	1.0		
GEORGETE (A;F) (25 months)	Feb2001-Jan2002	12	**2.2***	0.7	**0.0****
	Feb2002-Jan2003	12	0.7		
ESPERTA (A;F) (22 months)	Jun2002-May2003	12	**1.0***	0.2	**0.2****
	Jun2003-Feb2004	10	0.4		


Paulete (A;F) - WEST BORDER
33 Months


Esperta (A;F) - NORTHWEST BORDER
22 Months


James (A;M) - SOUTHEAST BORDER
29 Months


Georgete (A;F) - SOUTHEAST BORDER
25 Months



Tonha (A;F) - CENTRE
33 Months

Tina (A;F) - CENTRE
27 Months

Figure 3.4. Cumulative monthly areas of use (km²) of six lowland tapirs monitored for over 22 months in Morro do Diabo State Park, São Paulo, Brazil. Graphs indicate the point (month) where the home range of each tapir reached an asymptote. (A=adult; F=female; M=male).

3.3.1.6 Tapir Movements throughout the Fragmented Landscape of the Pontal do Paranapanema Region

Initial capture efforts were focused in the borders of Morro do Diabo to investigate if tapirs left the boundaries to feed on agricultural crops in the surroundings. All the radio-collared tapirs in the western border spent much of their active/foraging time along the Ribeirão Bonito stream and some left the boundaries of Morro do Diabo to explore the surrounding environments (Chapter 5 includes complete results on tapir habitat use and habitat selection).

Two radio-collared female tapirs - adult Xuxa and sub-adult Chu-Chu - were captured in pitfall traps placed ~500 m outside the western border of Morro do Diabo, in the middle of a small field of pasture. Throughout their periods of monitoring, these two females used to cross the agricultural and pastoral land landscape matrix outside Morro do Diabo to reach Ribeirão Bonito, a 4.2 km^2 forest fragment located 1,500 m from the western edge of Morro do Diabo. Tapirs only crossed the actual landscape matrix during evening and night hours. These visits to the Ribeirão Bonito forest fragment were fairly frequent. Chu-Chu was radio-tracked for 35 months and visited the forest fragment on 18 different occasions during monitoring periods. A total of 89 (30%) of the telemetry locations (N=294) obtained for Chu-Chu were in the area of the Ribeirão Bonito fragment. Xuxa was radio-tracked for three months and visited the fragment on three occasions. A total of eight (11%) of the telemetry locations (N=71) obtained for Xuxa were in the area of the Ribeirão Bonito fragment. During these visits, tapirs would usually stay in the forest fragment for periods from 1-8 days. However, from late January 1999 to early June 1999, all locations obtained for Chu-Chu were in the area of the forest fragment. The research team followed a sampling design and therefore did not monitor radio-collared tapirs every day. Consequently, it was not possible to determine if this female stayed in the fragment for the entire 4-month period.

Chu-Chu had the largest home range size of 14.2 km^2 (KDE95%) among all 19 radio-tracked tapirs, and this can be easily explained by her regular excursions outside Morro do Diabo (Figure 3.5.1). The home range size of Xuxa was 5.1 km^2 (KDE95%) but she was monitored for only three months, so this most probably does not reflect her true home range size (Figure 3.5.2). The 50% core areas of use of Chu-Chu (2 core units, 2.5 km^2) were located in between the edges of Morro do Diabo and of the Ribeirão Bonito fragment, while her 25% core area (1 core unit, 0.7 km^2) was located on the edge of Morro do Diabo. Both the 50% (2 core units, 0.5 km^2) and 25% (1 core unit, 0.2 km^2) core areas of use of Xuxa were located inside Morro do Diabo.

In the north western edge of Morro do Diabo, two tapirs (1 adult female and 1 adult male) were monitored from January 2002 to March 2004. The female (Esperta) was monitored for

22 months, and the male (Dedinho) for only two months. Both these tapirs regularly left the boundaries of Morro do Diabo to explore the surrounding sugar cane plantations for short periods of time. Both tapirs were captured in pitfall traps built right outside the forest in the immediate edge of Morro do Diabo. Although there were some small forest fragments of 2,200 m from that edge of Morro do Diabo, these two tapirs never visited those fragments and their 50% and 25% core areas of use were located inside Morro do Diabo and away from the border.

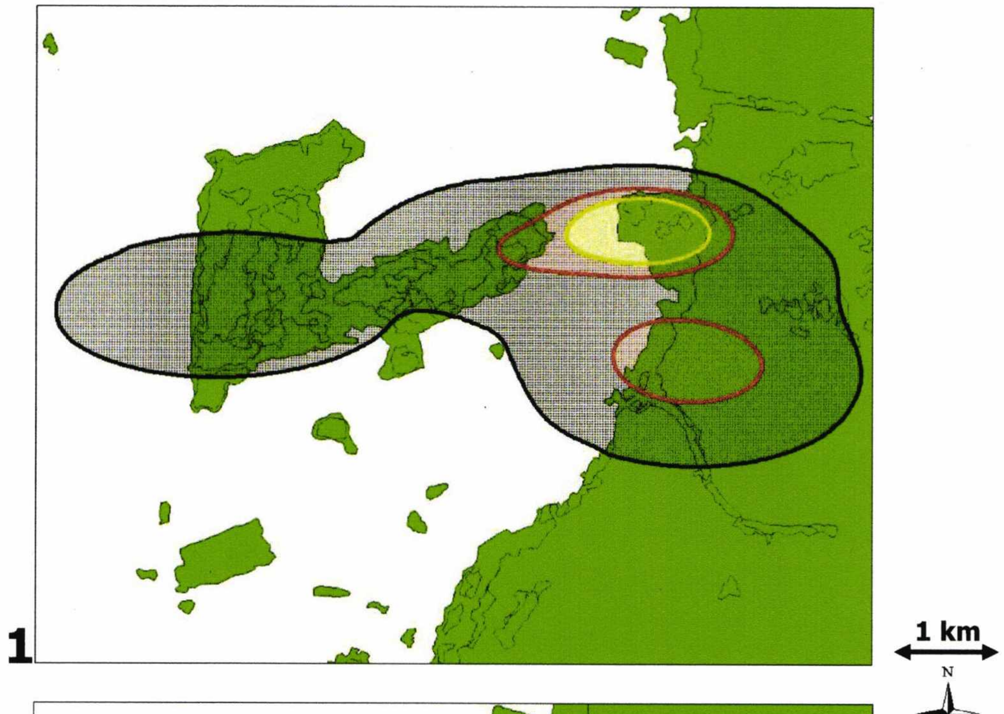


Figure 3.5. 1- Map of home range and core areas of use of sub-adult female Chu-Chu. 2- Map of home range and core areas of use of adult female Xuxa. (BLACK=KDE95%; RED=KDE50%; YELLOW=KDE25%). Maps show the western edge of Morro do Diabo State Park to the right and the Ribeirão Bonito forest fragment (4.2 km²) to the left. Figures 2.5 and 2.6 (Chapter 2) provide further reference on the location of Morro do Diabo State Park.

3.3.2 Intra-Specific Interactions

3.3.2.1 Home Range Overlap

The mean home range overlap calculated for 11 tapirs (8 females and 3 males, or 9 adults and 2 sub-adults) monitored in the long-term in Morro do Diabo was 37%. The mean home range overlap between the sexes was: 33.4% for pairs of females, 34.9% for pairs of female-male, and 43.2% for pairs of males (Table 3.13). There was no difference in home range overlap when comparing pairs of females, pairs of female-male, and pairs of males (H=1.473; DF=2; P=0.479). The mean home range overlap between age classes was: 32.2% for pairs of adults, 39% for pairs of sub-adults, and 37.2% for pairs of adult-sub-adult (Table 3.14). There was no difference in home range overlap when comparing pairs of adults, pairs of sub-adults, and pairs of adult-sub-adult (F=0.412; DF=2; P=0.665).

Table 3.13. Intra- and inter-sexual home range overlap (% and km²) in Morro do Diabo State Park, São Paulo, Brazil. (N=number of tapirs; F=female; M=male; Min=Minimum; Max=Maximum).

Female - Female (N=8 tapirs; 10 pairs)		**Female - Male** (N=14; 13 pairs; 9F & 5M)		**Male - Male** (N=2; 1 pair)	
Overlap (%)	**Overlap** (km²)	**Overlap** (%)	**Overlap** (km²)	**Overlap** (%)	**Overlap** (km²)
33.4 Min 4.6 Max 82.1	**2.0**	**34.9** Min 6.9 Max 92.3	**1.5**	**43.2** Min 36.6 Max 49.8	**1.9**

Table 3.14. Intra- and inter-age home range overlap (% and km²) in Morro do Diabo State Park, São Paulo, Brazil. (N=number of tapirs; A=adult; SA=sub-adult; Min=Minimum; Max=Maximum).

Adult - Adult (N=11 tapirs; 14 pairs)		**Sub-Adult - Sub-Adult** (N=4; 4 pairs)		**Adult - Sub-Adult** (N=6; 6 pairs; 3A & 3SA)	
Overlap (%)	**Overlap** (km²)	**Overlap** (%)	**Overlap** (km²)	**Overlap** (%)	**Overlap** (km²)
32.2 Min 4.6 Max 92.3	**1.2**	**39.0** Min 9.2 Max 82.8	**3.0**	**37.2** Min 14.4 Max 82.1	**2.2**

3.3.2.2 Overlap of Core Areas of Use

The mean overlap of core areas of use calculated for the same 11 tapirs was 19.5% at the 50% level, and 21.2% at the 25% level. The mean overlap of core areas between pairs of females was 21.4% at the 50% level, and 23.1% at the 25% level. The mean overlap of core areas between pairs of female-male was 18.9% at the 50% level, and 19.4% at the 25% level. The mean overlap of core areas between pairs of males was 12.9% at the 50% level, and there was no overlap at the 25% level (Table 3.15). There were no differences in overlap of core areas of use between pairs of females, pairs of female-male, and pairs of males either at the 50% (F=0.230; DF=2; P=0.797) or at the 25% level (t=0.286; DF=6; P=0.784). The mean overlap of core areas between pairs of adults was 17.2% at the 50% level, and 24% at the 25% level. The mean overlap of core areas between pairs of sub-adults was 32% at the 50% level, and there was no overlap at the 25% level. The mean overlap of core areas between pairs of adult-sub-adult was 22.4% at the 50% level, and 13% at the 25% level (Table 3.16). There were no differences in overlap of core areas of use between pairs of adults, pairs of sub-adults, and pairs adult-sub-adult either at the 50% (F=0.826; DF=2; P=0.453) or at the 25% level (t=0.760; DF=6; P=0.476) levels.

Table 3.15. Intra- and inter-sexual overlap of core areas of use (KDE50% and KDE25%, % and km^2) in Morro do Diabo State Park, São Paulo, Brazil. (N=number of tapirs; F=female; M=male; Min=Minimum; Max=Maximum).

50%	**Female - Female** (N=6 tapirs)		**Female - Male** (N=8; 5F & 3M)		**Male - Male** (N=2)	
	Overlap (%)	**Overlap** (km^2)	**Overlap** (%)	**Overlap** (km^2)	**Overlap** (%)	**Overlap** (km^2)
	21.4 Min 1.6 Max 45.1	**0.3**	**18.9** Min 0.01 Max 52.2	**0.1**	**12.9** Min 12.3 Max 13.5	**0.1**
25%	**Female - Female** (N=3 tapirs)		**Female - Male** (N=4; 2F & 2M)		**Male - Male** (N=2)	
	Overlap (%)	**Overlap** (km^2)	**Overlap** (%)	**Overlap** (km^2)	**Overlap** (%)	**Overlap** (km^2)
	23.1 Min 6.0 Max 45.5	**0.1**	**19.4** Min 2.8 Max 46.2	**0.03**	---	---

Table 3.16. Intra- and inter-age overlap of core areas of use (KDE50% and KDE25%, % and km^2) in Morro do Diabo State Park, São Paulo, Brazil. (N=number of tapirs; A=adult; SA=sub-adult; Min=Minimum; Max=Maximum).

50%	**Adult - Adult** (N=9 tapirs)		**Sub-Adult - Sub-Adult** (N=2)		**Adult - Sub-Adult** (N=3; 2A & 1SA)	
	Overlap (%)	**Overlap** (km^2)	**Overlap** (%)	**Overlap** (km^2)	**Overlap** (%)	**Overlap** (km^2)
	17.2 Min 0.01 Max 52.2	**0.1**	**32.0** Min 31.7 Max 32.2	**0.8**	**22.4** Min 5.6 Max 45.1	**0.2**
25%	**Adult - Adult** (N=6 tapirs)		**Sub-Adult - Sub-Adult** (N=2)		**Adult - Sub-Adult** (N=2; 1A & 1SA)	
	Overlap (%)	**Overlap** (km^2)	**Overlap** (%)	**Overlap** (km^2)	**Overlap** (%)	**Overlap** (km^2)
	24.0 Min 2.8 Max 46.2	**0.03**	---	---	**13.0** Min 6.0 Max 19.9	**0.04**

3.3.2.3 Social Organisation

Based on results of home range overlap and overlap of 50% and 25% core areas of use between pairs of individual tapirs (Table 3.17), I examined possible relations among different individual tapirs and made inferences about social organisation in three sections of Morro do Diabo (western border, centre, and south eastern border). These inferences were made without information on genetic relatedness among individuals.

In the western border of Morro do Diabo, three female tapirs, including two adults (Joana and Paulete) and one sub-adult (Chu-Chu), exhibited extensive home range overlap amongst themselves: 69% overlap between Joana and Chu-Chu, 66% overlap between Joana and Paulete, and 49% overlap between Paulete and Chu-Chu. The core areas of use of adult Joana and sub-adult Chu-Chu also overlapped extensively: 45% of overlap at the 50% level, and 20% at the 25% level. Similarly, the core areas of use of Joana and Paulete overlapped: 29% at the 50% level, and 45% at the 25% level. The core areas of use of Paulete and Chu-Chu presented an overlap of 25% at the 50% level, but there was no overlap at the 25% level. These results indicate that the sub-adult female Chu-Chu could be a 1-3 year old offspring of adult female Joana, who was staying together with her mother for a few years before dispersing from the area to establish her own home-range.

Only two sub-adult males were radio-tracked in the western border (Luizinho and João) were sub-adults, which limited opportunities to identify adult mating pairs in the area. In addition, these two sub-adults were monitored for very short periods of time and not concurrently, which limited the analysis of area overlap between them and the females in the area. However, results of home range overlap between Luizinho and four females in the area, including three adult females (Joana, Paulete, and Xuxa), and one sub-adult (Chu-Chu) show that the most extensive home range overlap occurred between Luizinho and Joana (36%). There was no overlap of core areas of use. Therefore, there is the possibility that Luizinho could also be Joana's offspring. There was also extensive home range overlap between Chu-Chu and Luizinho (72%), which corroborates the indication that they could be both offspring of Joana, still living in the vicinity of their mother's home range prior to dispersal. Another possibility is that Chu-Chu and Luizinho formed a young mating pair, in which case only one of them would be Joana's offspring, most probably Chu-Chu. Also in the western area of Morro do Diabo, the home ranges of sub-adult male João and sub-adult female Patrícia, showed an extensive home range overlap of 83%, which could indicate that they were either offspring of the same adult female, or a young mating pair.

In the centre of Morro do Diabo, the home ranges of adult females Mama, Tina and Tonha, were all monitored concurrently and over the long-term, and did not overlap. In fact, Tina's home range was actually 4 km from her capture site, to which she went back on only a few occasions during the time of her monitoring. The most extensive home range overlap between the sexes in this area of Morro do Diabo was 92%, between adult female Mama and adult male Chico, followed by 55% between adult female Tonha and adult male Cidão. Mama and Chico also presented extensive overlap of their core areas of use: 52% at the 50% level, and 46% at the 25% level. Tonha and Cidão showed an overlap of 51% at the 50% level, but a much smaller overlap of 4% at the 25% level. Mama and Cidão, as well as Tonha e Chico exhibited very little home range overlap. These results indicate that Mama and Chico, as well as Tonha and Cidão might be reproductive pairs in that part of Morro do Diabo. Another aspect that could corroborate this inference is that both Mama's and Chico's home ranges overlapped with sub-adult Julia's home range, which could be an indication that Julia might be a previous offspring of Mama and Chico. Mama and Julia showed an extensive home range overlap of 45%. Chico and Julia showed a home range overlap of 33%. Mama, Chico, and Julia were all captured and radio-collared in the same wooden corral in the central area of Morro do Diabo.

In the southeast border of Morro do Diabo, only one adult female - Georgete - and one adult male - James Bond - were radio-tracked concurrently for long periods. The home ranges of these two individuals showed an overlap of 45%, and their core areas of use showed 0.02% of overlap at the 50% level. However, the percentage of home range overlap between these two adult tapirs was not as high as the extent of overlap between males and females in the centre of Morro do Diabo. Therefore, there is no strong evidence that Georgete and James Bond formed a reproductive pair, although the possibility cannot be discarded.

Table 3.17. Home range overlap (HR; KDE95%, % and km^2) and overlap of core areas of use (CA; KDE50% and KDE25%, % and km^2) between intra- and inter-sexual pairs of tapirs in different sections of Morro do Diabo State Park (MDSP), São Paulo, Brazil. (N=number of tapirs; F=female; M=male; A=adult; SA=sub-adult)

Female-Female (N=8)	**Area MDSP**	**HR Overlap KDE95%**		**CA Overlap KDE50%**		**CA Overlap KDE25%**		**Timeframe of Radio-Tracking**
		%	km^2	%	km^2	%	km^2	
JOANA (A;F) X PAULETE (A;F)	West Border	61.8	2.7	21.7	0.2	21.0	0.05	Both radio-tracked in the long-term
PAULETE (A;F) X JOANA (A;F)		65.6		29.5		45.5		
JOANA (A;F) X CHU-CHU (SA;F)	West Border	68.7	3.0	45.1	0.3	19.9	0.04	Both radio-tracked in the long-term
CHU-CHU (SA;F) X JOANA (A;F)		21.3		13.7		6.0		
PAULETE (A;F) X CHU-CHU (SA;F)	West Border	49.3	2.0	25.0	0.1	---	---	Both radio-tracked in the long-term
CHU-CHU (SA;F) X PAULETE (A;F)		14.4		5.6		---		
PATRICIA (SA;F) X CHU-CHU (SA;F)	West Border	34.7	3.9	31.7	0.8	---	---	Both radio-tracked in the long-term
CHU-CHU (SA;F) X PATRICIA (SA;F)		27.5		32.2		---		
JOANA (A;F) X XUXA (A;F)	West Border	36.5	1.6	---	---	---	---	Xuxa (A;F) radio-tracked for only 3 months
XUXA (A;F) X JOANA (A;F)		31.7		---		---		
PAULETE (A;F) X XUXA (A;F)	West Border	11.7	0.5	---	---	---	---	Xuxa (A;F) radio-tracked for only 3 months
XUXA (A;F) X PAULETE (A;F)		9.5		---		---		
CHU-CHU (SA;F) X XUXA (A;F)	West Border	29.4	4.2	---	---	---	---	Xuxa (A;F) radio-tracked for only 3 months
XUXA (A;F) X CHU-CHU (SA;F)		82.1		---		---		
JULIA (A;F) X MAMA (A;F)	Centre	11.4	0.8	1.6	0.03	---	---	Both radio-tracked in the long-term
MAMA (A;F) X JULIA (A;F)		45.2		7.6		---		
BABY (A;F) X MAMA (A;F)	Centre	5.8	0.1	---	---	---	---	Baby (A;F) radio-tracked for only 4 months
MAMA (A;F) X BABY (A;F)		4.6		---		---		
BABY (A;F) X JULIA (A;F)	Centre	47.4	0.7	---	---	---	---	Baby (A;F) radio-tracked for only 4 months
JULIA (A;F) X BABY (A;F)		9.5		---		---		
Male-Male (N=2)	**Area MDSP**	**HR Overlap KDE95%**		**CA Overlap KDE50%**		**CA Overlap KDE25%**		**Timeframe of Radio-Tracking**
		%	km^2	%	km^2	%	km^2	
CHICO (A;M) X CIDAO (A;M)	Centre	36.6	1.9	12.3	0.1	---	---	Both radio-tracked in the long-term
CIDAO (A;M) X CHICO (A;M)		49.8		13.5		---		

Female-Male (N=14; 9F & 5M)	**Area MDSP**	**HR Overlap KDE95%**		**CA Overlap KDE50%**		**CA Overlap KDE25%**		**Timeframe of Radio-Tracking**
		%	km^2	%	km^2	%	km^2	
LUIZINHO (SA;M) X JOANA (A;F)	West Border	34.0	1.6	---	---	---	---	Luizinho (SA;M) radio-tracked for only 3 months
JOANA (A;F) X LUIZINHO (SA;M)		35.6		---		---		
LUIZINHO (SA;M) X PAULETE (A;F)	West Border	21.1	1.0	---	---	---	---	Luizinho (SA;M) radio-tracked for only 3 months
PAULETE (A;F) X LUIZINHO (SA;M)		23.4		---		---		
LUIZINHO (SA;M) X CHU-CHU (SA;F)	West Border	72.5	3.3	---	---	---	---	Luizinho (SA;M) radio-tracked for only 3 months
CHU-CHU (SA;F) X LUIZINHO (SA;M)		23.6		---		---		
LUIZINHO (SA;M) X XUXA (A;F)	West Border	34.9	1.6	---	---	---	---	Luizinho (SA;M) radio-tracked for only 3 months
XUXA (A;F) X LUIZINHO (SA;M)		31.8		---		---		
JOAO (SA;M) X PATRICIA (SA;F)	West Border	82.8	3.4	---	---	---	---	Joao (SA;M) radio-tracked for only 2 months
PATRICIA (SA;F) X JOAO (SA;M)		30.4		---		---		
JOAO (SA;M) X CHU-CHU (SA;F)	West Border	31.5	1.3	---	---	---	---	Joao (SA;M) radio-tracked for only 2 months
CHU-CHU (SA;F) X JOAO (SA;M)		9.2		---		---		
CHICO (A;M) X MAMA (A;F)	Centre	33.2	1.7	23.1	0.2	24.2	0.05	Both radio-tracked in the long-term
MAMA (A;F) X CHICO (A;M)		92.3		52.2		46.2		
CHICO (A;M) X TONHA (A;F)	Centre	22.5	1.2	9.1	0.1	---	---	Both radio-tracked in the long-term
TONHA (A;F) X CHICO (A;M)		37.9		21.8		---		
CHICO (A;M) X JULIA (A;F)	Centre	32.7	1.7	5.2	0.04	---	---	Both radio-tracked in the long-term
JULIA (A;F) X CHICO (A;M)		22.9		2.5		---		
CIDAO (A;M) X TONHA (A;F)	Centre	44.9	1.7	23.7	0.2	2.8	0.005	Both radio-tracked in the long-term
TONHA (A;F) X CIDAO (A;M)		55.5		51.4		4.3		
CIDAO (A;M) X MAMA (A;F)	Centre	9.1	0.3	---	---	---	---	Both radio-tracked in the long-term
MAMA (A;F) X CIDAO (A;M)		18.6		---		---		
CIDAO (A;M) X JULIA (A;F)	Centre	13.4	0.5	---	---	---	---	Both radio-tracked in the long-term
JULIA (A;F) X CIDAO (A;M)		6.9		---		---		
JAMES (A;M) X GEORGETE (A;F)	Southeast Border	45.0	0.8	---	---	---	---	Both radio-tracked in the long-term
GEORGETE (A;F) X JAMES (A;M)		40.4		---		---		

3.4 Discussion

3.4.1 Use of Radio-Telemetry for Studying Tapirs

Tapirs are mostly solitary, nocturnal, secretive animals, a combination of factors that makes it extremely complicated to study them through direct observations. Thus, radio-telemetry has been widely recognised as one of the most appropriate methodologies for the study of tapirs. This study in the Atlantic Forests of Morro do Diabo in Brazil was the first to apply radio-telemetry to monitor lowland tapirs over the long-term. This study included a large sample size of 19 radio-tracked tapirs, most of which were monitored over the long-term. The radio-telemetry data gathering techniques employed in this study, while relatively costly and labour-intensive, resulted in very detailed and precise results on several parameters including tapir ranging behaviour among others.

3.4.1.1 Tapir Capture and Chemical Restraint

One of the main limiting factors to using radio-telemetry for tapirs is placing radio-collars on these highly elusive, nocturnal animals. This requires the capture and immobilisation of the individuals. As a result of the more widespread use of radio-telemetry for tapir studies over the last 15 years, the need for appropriate protocols for the capture and immobilisation of free-ranging tapirs has arisen.

The capture of tapirs in Morro do Diabo went relatively smoothly once the team determined that salt was the most appropriate bait and the optimal capture techniques for the area. Pitfalls and wooden corrals were considered to be the most appropriate capture methods for tapirs in Morro do Diabo. Both these traps had the main advantage that tapirs were physically restrained and could be manipulated once inside the trap. This gave the team full control of the recovery and release processes. Another advantage of these methods was that rapid anaesthetic induction was not a concern when using pitfalls and corrals. Therefore, once the animal was observed inside the trap, veterinarians had time to select anaesthetic agents that were most appropriate for the situation. It was possible to estimate of the size of the animal more precisely, and evaluate its behaviour and level of stress, all important factors to determine the most appropriate anaesthetic protocol to be employed. While pitfall traps did not require the use of bait, the success of this capture method was fully dependant on the placement of the pitfall in frequently used tapir paths. In contrast, wooden corrals depended heavily on the use of bait and on tapirs becoming comfortable to going inside the trap to lick the salt, a very long process that sometimes took more than a year before these traps were ready for captures.

In terms of anaesthetic protocols, 44 tapir immobilisations and manipulations were carried out during this long-term study in Morro do Diabo, and the chemical restraint of tapirs proved to be quite challenging. All these tapir manipulations were different from one another given that the anaesthetic agents applied appeared to have different effects on different individual tapirs. As a consequence, the research team was under no circumstances able to determine a clear pattern of tapir cardiac and respiratory rates during anaesthesia. Possible explanations for this include the different metabolisms of different individuals, the amount of time spent inside the trap before manipulation, the time since last food consumption, and temperature among other factors (P.R. Mangini, personal communication). The respiratory rate, type and amplitude are the most important parameters to monitor anaesthetic depression and identify emergencies. The most common emergencies during tapir immobilisations include hypothermia, hyperthermia, bradicardia and apnoea (Medici *et al.* 2007b). Tapirs are capable of going into long periods of physiological apnoea while swimming, therefore short periods of apnoea during chemical restraint tend to be less compromising for the species. However, the veterinarian responsible for a tapir immobilisation must be capable of noticing an apnoea and rapidly taking the necessary measures.

The data on tapir anaesthesia monitoring during immobilisations in Morro do Diabo was constantly evaluated and anaesthetic protocols adjusted accordingly in order to guarantee the well being of the animals under anaesthesia, as well as the safety of the members of the research team. All tapir captures and immobilisations were carried out in the presence of at least one veterinarian specialised in wildlife medicine, who through this project had acquired many years of experience with the immobilisation and handling of free-ranging lowland tapirs. Capture stress and emergencies are intrinsic risks of the handling of wild animals. However, well-planned capture procedures and the participation of a well-prepared veterinarian can significantly reduce these risks.

3.4.1.2 Timeframe of Telemetry Monitoring for Tapir Studies

Another limiting factor to applying radio-telemetry and obtaining precise estimates of parameters of tapir ranging behaviour, particularly home range size, is the timeframe of monitoring. Tapirs are wide-ranging species with large spatial requirements. Thus, telemetry studies on tapirs must be planned for and carried out over the long-term.

The tapir telemetry data gathered during this study have shown that a minimum of ~300 locations and 20 months of data collection are necessary to determine home range size for adult lowland tapirs, while for sub-adults, a minimum of 32 months is needed. This information is particularly valuable for the sampling design and budgeting of future telemetry studies on tapirs. Indeed, this information has already been extremely helpful for the design of the Lowland Tapir Research and Conservation Programme established in the Brazilian Pantanal in early 2008. In the Pantanal, I am using GPS telemetry to study tapirs. Based on data from Morro do Diabo, I have programmed the GPS units according to a schedule of fixes that will make their batteries last for 20 months. For the sub-adults in the Pantanal, I will need to recapture them after 20 months of data collection and replace their collars in order to monitor them for 20 more months.

3.4.2 Methodological Considerations on the Estimate of Tapir Home Range Size

Both Kernel Density Estimator (KDE95%) and Minimum Convex Polygon (MCP95%) were used to estimate tapir home range size in Morro do Diabo. While KDE is widely recognised as the most reliable method to estimate home range (Powell 2000; Kernohan *et al.* 2001; Hemson *et al.* 2005), I did not observe significant differences between tapir home range sizes estimated by KDE and MCP. Tobler (2008) also compared lowland tapir home range estimates obtained by KDE and MCP and observed that the two estimators were very similar. Nevertheless, KDE estimates have the further advantage of providing further descriptions of the internal structure of the home range, allowing for the identification of core areas of use (Hooge *et al.* 2001).

3.4.3 Spatial Ecology of Tapirs in Morro do Diabo State Park

3.4.3.1 Home Range Size

The estimates of lowland tapir home range size reported in the literature vary widely (Chapter 2, Table 2.6). This variation can be explained by differences in environments and habitat types studied, as well as by different levels of habitat conservation, in turn reflecting different carrying capacities in different habitats found within the species distribution range (Eisenberg 1997; Medici *et al.* 2007a). The variation can also be attributed to different methods of estimating used, the timeframe of monitoring, and the number of individuals monitored. At any rate, tapirs are large-bodied, wide-ranging mammals that usually require very large home ranges (Williams 1978; Williams 1984; Foerster 1998; Herrera *et al.* 1999; Foerster & Vaughan 2002; Noss *et al.* 2003; Ayala 2003; Lizcano & Cavelier 2004; Tobler 2008; Abdul Ghani 2009; Naranjo 2009). This long-term lowland tapir study in Morro do Diabo further supports these findings.

The sizes of the individual tapir home ranges in Morro do Diabo varied from 1.1-14.2 km^2, resulting in an overall mean home range size of 4.7 km^2 (Group 2, 14 tapirs radio-tracked from 8-36 months). Thus, the home range size of tapirs in Morro do Diabo was found to be much larger than in other areas where the species was previously studied. In Kaa-Iya del Gran

Chaco National Park, Bolivia, a telemetry study showed a mean home range size of 2.5 km² (Noss *et al.* 2003). In Los Amigos Research Station in the Peruvian Amazon lowland tapirs used a mean home range of 2.6 km² (Tobler 2008). Only two other telemetry studies have observed larger lowland tapir home ranges than in Morro do Diabo. Tarcísio Silva Jr. (1997, unpublished results) obtained a home range of ~39 km² in Brasília National Park, Brazil, while Herrera *et al.* (1999) showed a home range of 16.4 km² in the Amazonian forests of the Lago Caiman Noel Kempff Mercado National Park, Bolivia. However, both these studies relied on very small sample sizes, involving the radio-tracking of only one individual tapir each, and were based on very few locations (20 and 10, respectively).

The large tapir home range sizes in the Atlantic Forests of Morro do Diabo might be explained by one or more factors. First, it might be associated with the extensive forest fragmentation in the Pontal do Paranapanema Region. Both Kaa-Iya del Gran Chaco National Park (34,400 km²) in Bolivia, as well as Los Amigos (1,400 km²) in Peru, consist of expanses of contiguous habitat. In contrast, Morro do Diabo is a relatively small forest fragment of no more than 370 km² immersed in a landscape matrix of agricultural and pastoral land. Forest reduction and fragmentation are generally accompanied by loss of habitat diversity, which in turn affects resource diversity and availability (Wright & Duber 2001; Tabarelli *et al.* 2004). There is growing evidence that the availability of fruit in forest fragments is lower when compared to continuous tracts of tropical forest (Terborgh 1986; Terborgh 1992). A suite of resource-related factors specific to different habitat types, such as spatial distribution of fruit sources, total fruit availability, seasonal fruit availability, and severity of fruit scarcity periods, will affect habitat use, spatial requirements, and ultimately the persistence of frugivore populations in habitat fragments (Keuroghlian & Eaton 2008). Although recent, the process of destruction and fragmentation of the Atlantic Forest of the Interior in the Pontal do Paranapanema Region have most certainly led to a reduction in the habitat diversity of Morro do Diabo. In addition, before its establishment as a protected area in 1986, Morro do Diabo had already suffered from severe processes of habitat degradation. These included the construction of both a railway and a highway that crossed Morro do Diabo, causing the clearing of several patches of forest within the area of Morro do Diabo for the extraction of timber, selective logging of valuable hard woods, and several major fire events (Faria & Pires 2006). The combination of all these factors has most certainly caused a reduction in the carrying capacity of Morro do Diabo.

A second factor may be the very heterogeneous, semi-deciduous habitats of Morro do Diabo. In these habitats, primary production is lower and more erratic than in more moist forests (Cullen *et al.* 2001a). Habitat heterogeneity results in different fruiting periods for different plant species (Durigan & Franco 2006). Lowland tapirs feed accordingly to the availability and abundance of food resources (Bodmer 1990a; Salas 1996). Therefore tapirs in Morro do Diabo need their home ranges to include large expanses of forest so that they can fulfil their nutritional requirements. In addition, the availability of water in semi-deciduous habitats is very low (Cullen *et al.* 2001a). Some areas of Morro do Diabo are extremely poor in water resources. With the exception of the Paranapanema River, which is a large, wide river, the other water courses in Morro do Diabo are small streams that during extreme dry seasons have their levels of water considerably reduced. Therefore, tapirs in Morro do Diabo need their home ranges to be large enough to include a permanent source of water.

The third factor is methodological. It is directly related to the timeframe of monitoring and sample size of the study in Morro do Diabo. A large number of different individual tapirs were monitored over the long-term. Therefore, the home range estimates obtained in Morro do Diabo may have been more precise relative to other studies. Some of the previous estimates of lowland tapir home range size were obtained from small datasets collected from just a few individuals monitored in the short-term. Tobler (2008) noted that due to the short duration of many of his lowland tapir datasets from the Peruvian Amazon, his home range size estimates were likely underestimated for some individuals.

Although there were no significant differences in home range size between the sexes, male tapirs in Morro do Diabo tended to have larger home ranges than females. This may be related to aspects of social organisation and mating system. Direct and indirect evidence from a field study on Baird's tapirs in Corcovado National Park in Costa Rica indicate that tapirs are not monogamous but probably facultative polygymous (C.R. Foerster, personal communication). This mating system predicts that a single male can mate with several females, without any restriction in the number of females per male, while females typically mate with only one male. Most large herbivores have a polygymous mating system, and males typically do not help females raise their young (Davies 1991). As a consequence, home ranges of male tapirs may incorporate larger areas so that they overlap with the home ranges of two or more females. Ayala (2003) observed that male lowland tapirs in Kaa-Iya del Gran Chaco National Park, Bolivia, had larger home ranges than females. Foerster & Vaughan (2002) observed that the home range of male Baird's tapirs in Corcovado were larger, but not significantly, than female home range.

In terms of age, although there were no significant differences in home range size between adults and sub-adults in Morro do Diabo, sub-adults tended to use larger home ranges. When sub-adult tapirs start to separate from their mothers they go through a process of exploring the areas in the surroundings and choosing where to disperse in order to establish their own home ranges. At any rate, it is important to note that the sample size of sub-adult individuals (N=4) was smaller than the adult sample size (N=15) and so final results for this age class may not be as accurate.

The lowland tapir home range size observed in Morro do Diabo was considerably larger than the other two Latin American tapir species. Lizcano & Cavelier (2004) used GPS telemetry to monitor mountain tapirs in Los Nevados National Park, Colombia. The authors estimated a mean home range size of 2.5 km² (KDE), while the mean home range size of Baird's tapirs studied via radio-telemetry in Corcovado National Park, Costa Rica, was 1.2 km² (MCP95%) (Foerster 1998; Foerster & Vaughan 2002). Williams (1984) estimated a mean home range size of 1.71 km² for Baird's tapirs in the dry forests of Santa Rosa National Park, also in Costa Rica. In contrast, a telemetry study on Malayan tapirs in Taman Negara, Malaysia, revealed very large home ranges of up to 12.75 km² (Williams 1978). A recent study on Malayan tapirs in Krau Wildlife Reserve, also in Malaysia, estimated a home range of ~10-15 km² (MCP100%) (Abdul Ghani 2009). Therefore, it appears that the home range of Malayan tapirs is much larger than the three Latin American tapir species.

3.4.3.2 Home Range Internal Structure: Core Areas of Use

Home range is typically characterised with descriptors of its size, shape and structure (Kenward 2001). Internal home range structure is usually described by size and distribution of core areas utilised with higher degrees of intensity (Poullé *et al.* 1994). Studies on various animal species show that, for a number of environment-related reasons, certain areas within the home range are more frequently used than others (Dixon & Chapman 1980; Springer 1982; Konecny 1989; Macdonald & Courtenay 1996). The core area of more intensive use may be related to the greater availability of food resources, water, and refuges (Burt 1943; Samuel *et al.* 1985; Samuel & Garton 1987), or in extent of home range overlap with neighbouring animals (Poullé *et al.* 1994).

Overall, tapirs in Morro do Diabo had very complex home range structures, including multiple core areas of use. The number of different core areas of use within the home range was as high as 17 core units at the 50% core level, and as many as 9 units at the 25% level. When summed up, the total size of these core areas comprised very small portions of the tapir home ranges. The 50% core areas of use comprised ~17% of the tapir home range, while the 25% core areas comprised no more than 6% of the home range. This pattern was very consistent for both sexes and different age classes. The core areas of use estimated for both sexes were very similar both in terms of size, as well as in terms of proportion of the entire home range. When looking at different age classes, while the 50% core areas of adults and sub-adults were also very similar in size; sub-adult tapirs had significantly larger 25% core areas of use than adult individuals. This is consistent with previous results on home range sizes for different age classes, where sub-adults, although not significantly, tended to have larger home ranges than adults. It is important to mention once more that the sample size of sub-adults was much smaller than for adults, which most probably affected the results.

Tobler (2008) recorded very similar results in terms of proportion of core areas of use within lowland tapir home ranges in the Peruvian Amazon: 50% core areas of use comprised ~19% of the range, and 25% core areas ~7%, with similar patterns obtained for both sexes. However, the home ranges of lowland tapirs in the Peruvian Amazon were less complex when compared with Morro do Diabo. Tobler (2008) noted that tapir home ranges included only 2-3 different core units. This difference might be once again explained by the habitat heterogeneity found in the semi-deciduous forests of Morro do Diabo (Durigan & Franco 2006). Lowland tapirs feed according to the availability and abundance of fruit, and might therefore establish their core areas of use in conjunction with the spatial and temporal heterogeneous distribution of fruiting trees. Another reason for the greater complexity of home range structure in Morro do Diabo might be related to the scarcity of water, and some of the core units may be associated with locations where water sources could be found. Lastly, the establishment of core areas of use by tapirs in Morro do Diabo did not seem to be related to the extent of home range overlap with neighbouring tapirs, given that results from this study have shown high percentages of overlap of core areas of use.

3.4.3.3 Seasonal Variations in Home Range and Core Areas of Use

In general, lowland tapirs in Morro do Diabo showed very little seasonal changes in size and location of home ranges and core areas of use. The sizes of tapir home ranges as well as core areas of use in wet and dry seasons in Morro do Diabo were very similar. Seasonal home ranges used in both wet and dry seasons consisted of ~55% of the entire home range of 4.7 km^2 (Group 2, 14 tapirs radio-tracked from 8-36 months). The small variation in location of seasonal home ranges was evidenced by a high percentage of overlap (70%) between home ranges used in wet and dry seasons. The sizes of the seasonal home ranges used by female and male tapirs were very similar for both seasons. Although the sizes of the home ranges calculated for different age classes were very similar in the dry season; sub-adult tapirs used significantly larger areas than adults in the wet season. The sizes of core areas intensively used by tapirs in wet and dry seasons were very similar. When examining seasonal core areas of use between the sexes and between different age classes, sub-adult tapirs had significantly larger core areas of use at the 50% level when compared to adults.

Other studies on tapirs have obtained similar results. Ayala (2003) found little seasonal variation in size of home range of lowland tapirs in Kaa-Iya del Gran Chaco National Park, Bolivia. Lizcano & Cavelier (2004) demonstrated that seasonal difference in home range size for mountain tapirs in Los Nevados National Park, Colombia, was not significant. Foerster & Vaughan (2002) found no seasonal changes in size or location of home ranges of Baird's tapirs in Corcovado National Park, Costa Rica.

The results from Morro do Diabo provided evidence that tapirs do not need to expand their ranges to meet seasonal deficiencies in habitat quality. Indeed, Tófoli (2006) studied the feeding ecology of lowland tapirs in the Atlantic Forests of the Pontal do Paranapanema Region, including Morro do Diabo and six small forest fragments in the surroundings, and observed that there were no differences in terms of consumption of fruit and fibrous materials in different seasons of the year. The absence of differences was once more explained by the heterogeneous, semi-deciduous habitats of Morro do Diabo (Durigan & Franco 2006), characterised by different fruiting periods of different plant species. Thus, the absence of seasonal differences in terms of consumption of fruit was most probably conditioned to habitat diversity (Tófoli 2006).

3.4.3.4 Tapir Movements throughout the Fragmented Landscape of the Pontal do Paranapanema Region

Approximately 17% of the Pontal do Paranapanema Region is still covered with Atlantic Forests. Besides Morro do Diabo, the fragmented landscape of the region includes the Black-Lion-Tamarin Ecological Station, which encompasses four forest fragments, and a multitude of other forest fragments scattered around both protected areas (Ditt 2002; Uezu *et al.* 2008). The landscape matrix is mainly composed of pasture land and agriculture (Uezu *et al.* 2008).

Tapirs are known to have the ability to traverse areas of low quality habitat, such as agricultural crops and pastoral lands, in order to move through the landscape matrix in between patches of forest (Flesher 2007). There have been a few records of lowland tapirs crossing patches of *Eucalyptus* plantations in between fragments of Atlantic Forest in Espírito Santo State, Brazil (A. Gatti, personal communication). In Malaysia, there have been sporadic records of Malayan tapirs crossing areas of palm oil estates, which seemed to occur primarily due to lack of choice as the animals seemed to be travelling from one forested area to the next (C. Traeholt, personal communication). Indeed, this study in Morro do Diabo further supports these observations.

Although not thoroughly quantified, I observed a considerable amount of tapir movement throughout the fragmented landscape of the Pontal do Paranapanema Region. Tapir signs including footprints, faeces and evidences of foraging were found in the landscape matrix in between the western and northern edges of Morro do Diabo and forest fragments in those areas. Two of the radio-collared tapirs in the western border travelled regularly between Morro do Diabo and a smaller forest fragment located at ~1,500 m from Morro do Diabo (Figure 3.5 in this Chapter). In the north western border, two radio-collared tapirs left the boundaries of Morro do Diabo regularly. Also by using signs, tapir pathways in between small forest fragments located to the north, northwest, and northeast of Morro do Diabo were identified. Overall, 12 possible tapir movement pathways were identified in the fragmented landscape of the Pontal do Paranapanema Region. Nevertheless, telemetry results were clear in showing that the radio-collared tapirs that used to cross the landscape matrix outside of the western and north western borders maintained their core areas of use inside Morro do Diabo, where they concentrated their main activities. While the tapir landscape crossings I am referring to were observed in rather short-scale (no further than 1.5-2.0 km) and apparently at low rates, they provided evidence of a tapir metapopulation scenario in the Pontal do Paranapanema Region.

During these landscape crossings, tapirs usually travelled through open areas of pasture land or agriculture, especially sugar cane plantations. In some instances, they crossed areas of forest regeneration, degraded forest corridors, and riparian forests along small rivers. Park rangers reported sightings of tapirs crossing the Paranapanema River in the southern limit of Morro do Diabo. There were several records of tapirs feeding on sugar cane, manioc and corn in the agricultural areas around Morro do Diabo, however this seemed to occur in a very small scale and never appeared to characterise a situation of human-tapir conflict.

3.4.4 Tapir Intra-Specific Interactions in Morro do Diabo State Park

3.4.4.1 Tapir Spatial Territoriality in Morro do Diabo State Park

Neighbouring tapirs in Morro do Diabo exhibited extensive home range overlap. This included extensive overlap between intra- and inter-sexual pairs, as well as between pairs of same and different age classes. In addition, several examples of extensive overlap of core areas of use were observed. The great majority of the tapirs radio-tracked in Morro do Diabo shared portions of their home ranges with several other tapirs. In the western border, one of the radio-tracked sub-adult females (Chu-Chu) shared portions of her home range with six other tapirs, including three adult females, other sub-adult female, and two sub-adult males. Two adult females in the same area (Joana and Paulete) each shared portions of their home ranges with four other tapirs. Two adult females radio-tracked in the centre of Morro do Diabo (Mama and Julia) each shared portions of their home ranges with four other tapirs.

Overall, the home range overlap between neighbouring tapirs was around 30%, although in some cases it was as high as 92%. The home range overlap could be even higher considering that I may not have been able to capture and monitor all tapirs in a given area. There were no significant differences in home range overlap between intra- and inter-sexual pairs, or between pairs of same and different age classes. It is important to mention that the analysis of home range overlap included only one pair of males and only one pair of sub-adult individuals, which might have affected some of these results.

The lowland tapir home range overlap in Morro do Diabo was fairly similar to previous results obtained for lowland and Baird's tapirs. Noss *et al.* (2003) obtained a mean home range overlap of 43.5% for lowland tapirs in Kaa-Iya del Gran Chaco National Park, Bolivia. In the same site in Bolivia, Ayala (2003) observed a home range overlap of 80% between an adult male and a juvenile male, and a 30% overlap between the same juvenile male and an adult female. Foerster & Vaughan (2002) observed a mean home range overlap of 33.2% for Baird's tapirs in Corcovado National Park, Costa Rica.

The overlap of core areas of use among tapirs in Morro do Diabo was around 20%, at both the 50% and 25% levels. Although there were no significant differences in overlap of core areas of use between intra- and inter-sexual pairs, pairs of females tended to present the most extensive overlap of core areas of use. The only pair of males included in the analysis - two adult individuals in the centre of Morro do Diabo - showed very little overlap of core areas of use at the 50% level and did not overlap at the 25% level. Similarly, there were no significant differences in overlap of core areas when comparing pairs of same and different age classes. However, the only pair of sub-adults included in the analysis - two females in the western border - showed an extensive overlap of core areas at the 50% level and did not overlap at the 25% level.

On the strength of the available evidence provided by the extensive home range overlap and, most importantly, the overlap of core areas of use, I found no indication whatsoever that spatial territoriality was present in the tapir population in Morro do Diabo. Territoriality usually arises when animals exhibit spatially oriented aggressive behaviour (Burt 1943; Brown & Orians 1970; Davies & Houston 1984; Maher & Lott 1995; Moorcroft *et al.* 1999; Jetz *et al.* 2004). The territory of an animal may be limited to a circumscribed area within the home range, where specific activities are performed (*e.g.* mating), or to core areas of use richest in resources, or may extend to the whole home range (Brown & Orians 1970). Tobler (2008) observed that lowland tapirs monitored through GPS telemetry in the Peruvian Amazon regularly walked along the boundaries of their home ranges, most probably defining their territory against other individuals by maintaining clear home range boundaries. This behaviour was not observed in Morro do Diabo although it would have been difficult to obtain this level of detail through the use of VHF telemetry. While tapirs in Morro do Diabo had well defined home ranges and lived within their boundaries, no evidence was found that they defended their areas against conspecifics. The only result of this study that could possibly might possibly indicate a certain level of spatial territoriality would be the small percentage of 50% core area overlap and complete absence of 25% core area overlap between male tapirs. This might also indicate polygamy. At any rate, this result was obtained from a single pair of adult males and, the spatial territoriality in this case, if present, was restricted to a very small portion of their home ranges.

3.4.4.2 General Inferences about Tapir Social Organisation in Morro do Diabo State Park

Baird's tapir offspring normally remain with their mother from 12-18 months (C.R. Foerster, personal communication). Once they separate, in most of the occasions, young tapirs stay in the vicinity of the mother's home range from 3-4 years prior to dispersal from the area and establishment of their own home ranges. Therefore, the ranging behaviour of tapirs in Corcovado included the establishment of so called "family units" where pairs of adult male and female tapirs maintained an almost entirely exclusive "territory" with no other resident adults over long periods of time, which they shared with 1-3 offspring from previous years (Foerster & Vaughan 2002). While extensive home range overlap was observed within the family units, very little overlap occurred between neighbouring tapir families (C.R. Foerster, personal communication). In the Peruvian Amazon, Tobler (2008) observed an almost 100% home range overlap between a male and a female lowland tapir. Genetic analysis carried out in Peru demonstrated that the two individuals were possibly siblings sharing their parents' territory. Both examples from Costa Rica and Peru provide evidence that the spatial and social organisation of tapirs in these areas was closely associated with the relatedness among different individuals, which most probably led to an increased level of tolerance among neighbours (Kitchen *et al.* 2005).

The lowland tapir study in Morro do Diabo did not indicate the establishment of such well defined family units. Nevertheless, results on home range overlap and overlap of core areas of use allowed for preliminary inferences on possible interactions and relatedness among individual tapirs, as well as for general observations about social organisation. It is important to clarify that these inferences were made without recourse to information on genetic relatedness among individuals. In the western border of Morro do Diabo, where I monitored seven different individual tapirs, there were indications of potential relatedness between an adult female (Joana) and two sub-adult individuals (female Chu-Chu and male Luizinho). Both these sub-adults could have been offspring of Joana. If Charles Foerster's concept of "family units" could be applied to Morro do Diabo, Chu-Chu and Luizinho could be sub-adult individuals with ~1-3 years of age, who were living within the home range of their mother Joana for a few years prior to dispersal and establishment of their own home ranges. Alternatively, the extensive home range overlap between Chu-Chu and Luizinho could indicate that they were a young mating pair. At the moment of her capture in June 1997, Joana appeared to be old enough to be one of the matriarchs in the western border. Still in the western area of Morro do Diabo, a pair of sub-adult male and sub-adult female exhibited extensive home range overlap, which could indicate that they were either offspring of the same adult female, or a young mating pair. In the centre of Morro do Diabo, where I monitored seven tapirs, very extensive inter-sexual overlap in home range as well as in core areas were observed for two pairs of female and male. These four individuals were adults in age of reproduction and could have been reproductive pairs in that section of Morro do Diabo.

Over the past few years since I concluded the telemetry study in Morro do Diabo, specific genetic markers for lowland tapirs have been well developed and made available. Biological samples from all the 35 tapirs captured in Morro do Diabo have been properly preserved. In the next few years, it will be possible to analyse the relatedness of these individuals and determine the social organisation of tapirs in Morro do Diabo in much more detail.

3.4.5 Lowland Tapir Spatial Requirements and Implications for Population Viability

Understanding the spatial requirements of animal populations across severely fragmented landscapes such as the Atlantic Forest is critical for the design and implementation of management and conservation strategies that can promote the survival and persistence of these populations over the long-term. Tapirs are wide-ranging species and have large spatial requirements. This long-term lowland tapir study in Morro do Diabo has further supported these observations. Tapirs in Morro do Diabo used very large home ranges. However, most essential in the context of examining the viability of tapir populations in the fragmented landscape of the Pontal do Paranapanema Region is the comparison of tapir spatial requirements found in Morro do Diabo, an Atlantic Forest fragment of 370 km^2, with large areas of contiguous habitat.

Some important patterns of tapir home range structure and intra-specific interactions observed in Morro do Diabo were very similar to what has been previously found for the species in non-fragmented habitats. The proportion of core areas of use in relation to home range size in Morro do Diabo was almost equal to what has been observed for the same parameter in the 1,400 km^2 of contiguous forests of Los Amigos Conservation Concession in the Peruvian Amazon (Tobler 2008). Likewise, the percentages of home range overlap observed in Morro do Diabo were very similar to estimates observed both at Los Amigos (Tobler 2008) and in Kaa-Iya del Gran Chaco National Park (34,400 km^2) in Bolivia (Noss *et al.* 2003). Nevertheless, the tapir home ranges in Morro do Diabo were considerably larger, almost twice as much, when compared to tapir home ranges observed in these large tracts of contiguous habitat (Ayala 2003; Noss *et al.* 2003; Tobler 2008).

As detailed previously, the main factors that might possibly explain the larger tapir home ranges in Morro do Diabo include the extensive habitat fragmentation, which led to a reduction in resource diversity and availability (Wright & Duber 2001; Tabarelli *et al.* 2004), as well as the characteristics of the semi-deciduous forests of Morro do Diabo, known for their low primary production and scarcity of water resources. Survival and reproduction are often food-limited. The abundance and predictability of food resources in time and space are important factors influencing spatial organisation (McLoughlin & Ferguson 2000). Food is often cited as an important limiting factor determining the home range size. Animals move and establish their home ranges in response to energetic needs, or to build a memory map of patches of food resources, or in response to the distribution of resting sites (South 1999). Tapirs in Morro do Diabo required large home ranges in order to obtain the resources they needed to fulfil their nutritional requirements and consequently survive and reproduce.

Nevertheless, tapirs in Morro do Diabo appeared to be fulfilling these requirements and the population appeared to be healthy and stable. In fact, tapirs in Morro do Diabo appeared to be reproducing rather well. During this study, I obtained various evidences of tapir reproduction including the capture of two adult female tapirs with young calves, four adult females that were lactating (pre or post parturition), and a number of other captured females presented vaginal secretions characteristic of reproductive periods. In some occasions, I captured females that had superficial wounds on their backs caused by mounting. In addition, members of the research team as well as other field researchers and park rangers reported regular sightings of female tapirs with calf.

Species with large spatial requirements generally cannot find sufficient food and other vital resources to survive and persist in small areas over the long-term (McNab 1963; Redford & Robinson 1991). Thus, the smaller forest fragments of the Pontal do Paranapanema Region may be too small to provide tapirs with the amount of space they require. Chiarello (1999) analysed the effects of the Atlantic Forest fragmentation on mammal communities, and observed that tapirs were present in large patches but not recorded in small ones. While Morro do Diabo benefits from a higher level of habitat diversity and conservation, the smaller forest fragments continue to suffer from habitat degradation.

Apart from Morro do Diabo State Park and the Black-Lion-Tamarin Ecological Station, all the other forest fragments in the Pontal do Paranapanema Region lie within private properties or Agrarian Reform landless settlements (owned by the State), therefore lacking legal protection. As a result, the impact of rural communities living in the vicinities of these small forest fragments - including erosion of forest edges by fires and cattle grazing, spread of aggressive weeds, and use of pesticides - have been seriously modifying forest structure and reducing habitat quality and carrying capacity for a number of species (Cullen 1997). Another consequence of habitat fragmentation is the reduction in diversity and availability of fruit (Terborgh 1986; Terborgh 1992), which is a serious limiting factor for the persistence of frugivore species such as tapirs. Tófoli (2006) analysed the impact of fragmentation of the Atlantic Forests of the Pontal do Paranapanema Region on the diet of tapirs and showed that tapirs in Morro do Diabo consumed significantly higher percentages of fruit and lower percentages of fibrous material when compared with tapirs in the smaller forest fragments. In addition, estimates of fruit species richness in the diet of tapirs indicated considerably higher fruit diversity in Morro do Diabo than in the forest fragments (Tófoli 2006). This indicates that the carrying capacity of these very small, largely degraded, non-protected forest fragments in the Pontal do Paranapanema Region might be indeed much lower than Morro do Diabo. In consequence, tapirs in these small areas might not be given the proper conditions to fulfil their large spatial requirements.

Small tapir populations in the Pontal do Paranapanema Region might be able to survive and persist over the long-term if they are connected to the Morro do Diabo. Preliminary results of a large scale lowland tapir survey currently underway throughout the entire range of the Atlantic Forest biome has already demonstrated that while tapirs appear to fulfil their spatial requirements and persist in some areas where habitat is reduced to small scattered fragments; they need to be able to resort to large forest fragments (Flesher 2007).

Evidences gathered during this study have shown that tapirs in the Pontal do Paranapanema Region move through the fragmented landscape in between different patches of forest. This indicates that the inter-habitat landscape matrix found in the Pontal do Paranapanema Region provides a satisfactory level of functional connectivity (Greenberg 1989; Sieving *et al.* 1996), in other words being fairly permeable for tapirs. During their landscape wonderings throughout the region, tapirs usually moved through areas of pasture land or agriculture. In other instances, they crossed areas of forest regeneration, degraded forest corridors, and riparian forests and swamps along small rivers. The fact that tapirs are mobile and can use these marginal non-natural habitat areas surrounding the forests where they live, most certainly helps them fulfil their spatial requirements in the smaller forest fragments. The tapir landscape crossings in between different patches of forest were observed in rather short-scales, and at apparently low rates. Nevertheless, they did provide evidence of a tapir metapopulation dynamics. This metapopulation can potentially allow tapirs in the small forest fragments to have access to the larger patches of forest, therefore promoting their persistence over the long-term. This is only deemed to be accurate if Morro do Diabo remains intact and effectively protected.

In addition to spatial requirements, population size is another critical determinant for the long-term persistence of animal species in severely fragmented landscapes. The next chapter focuses on estimating the size of the tapir populations in Morro do Diabo and surrounding Atlantic Forest fragments, providing essential information for predicting future population trends and assessing long-term viability of tapirs in the Pontal do Paranapanema Region.

Chapter 4

Determining Population Size

Photo by Anders Gonçalves da Silva

4.1 Introduction

Population size is considered to be the major determinant of species capacity for long-term persistence in a given area (Diamond *et al.* 1987; Newmark 1987; Pimm *et al.* 1988; Richman *et al.* 1988; Soulé *et al.* 1988; Berger 1990; Schoener & Spiller 1992; Foufopoulos & Ives 1999). Population size is a critical demographic attribute and the single most important parameter to determine extinction risk (Shaffer 1981; Gilpin & Soulé 1986; Lacy 1993; Lacy 2000; Shaffer *et al.* 2000; Aurambout *et al.* 2005). Determining extinction risk is at the heart of conservation biology (Burgman *et al.* 1993; Fagan *et al.* 2001; Fieberg & Ellner 2001; Beissinger & McCullough 2002). Population size is also the most important parameter for predicting future population trends and assessing population viability (Shaffer 1981; Gilpin & Soulé 1986). Most species-specific conservation efforts require reliable estimates of population size for making management decisions, establishing conservation priorities, and monitoring the success of conservation strategies (Matter 2000).

The size of animal populations is a particularly important factor in fragmented habitats. Fragmented habitats usually fail to provide the necessary resources to support species assemblages found in the intact ecosystem, which in turn leads to a general reduction in the number of individuals that can be supported (Lovejoy *et al.* 1984; Quinn & Hastings 1987; Bierregaard *et al.* 1992; Burkey 1993; Kattan & Alvarez-Lopez 1996). Since the 1980's, the understanding of the different processes that may bring small populations to extinction has increased considerably and is now well known as the "small population paradigm" (Terborgh & Winter 1980; Goodman 1987; Pimm *et al.* 1988; Berger 1990; Caughley 1994; Newmark 1994; Mace & Kershaw 1997; McKinney 1997; Belovsky *et al.* 1999; Foufopoulos & Ives 1999). The contention that small, isolated populations are more vulnerable to extinction has a sound theoretical basis in both demography and population genetics (Shaffer 1981; Lande 1988; Roelke *et al.* 1993; Lande 1995; Lynch & Lande 1998). At small population size, demography plays a critical role in population persistence (Goodman 1987; Nunney & Campbell 1993; Lande 1995; Lindenmayer & Lacy 1995). Small populations are more sensitive to stochastic events, such as fires or epidemic outbreaks, which could rapidly drive a population to extinction (Lacy 1993; Lacy 2000; Aurambout *et al.* 2005). Likewise, small, isolated populations are more susceptible to genetic drift, which could also lead, in the case of severe inbreeding, to population extinctions (Templeton *et al.* 1990). Overall, the chance of extinction increases exponentially with decreasing population size and increasing population isolation. In addition, population size has implications for population structure and dynamics, as well as community-level patterns (Matter 2000). The size of a population is integral to the concepts of density-dependence (Ray & Hastings 1996), population regulation (Clutton-Brock *et al.* 1985), as well as the functional and numerical responses of predators to prey (Morgan *et al.* 1997).

Making accurate estimates of population size is very difficult. Direct counts of animal populations are exceptionally difficult, if not impossible, to obtain. Animals are frequently difficult to capture or observe, and the associated costs and effort of making absolute counts are prohibitive (Gittleman 1996). Thus, animal ecologists have no other alternative but to rely on indirect methods that provide indices of population abundance and then derive or estimate population size. Some examples of indirect methods used for the estimate of animal abundance include radio-telemetry, camera-traps, line-transect sampling, track and dung counts among others (Emmons 1987; Emmons 1988; Konecny 1989; Ludlow & Sunquist 1987; Jewell *et al.* 2001; Maffei *et al.* 2002; Noss *et al.* 2003; Lizcano 2006; Cullen 2007; Alibhai *et al.* 2008).

Large terrestrial mammals - such as tapirs - occur at lower population densities when compared to small mammals (Eisenberg 1980). Thus, while estimates of lowland tapir density reported in the literature vary, due to both differences in the methods of estimation used and in the environments and types of habitat studied, they tend to occur naturally at low densities (Cullen *et al.* 2000; Aquino *et al.* 2001; Aquino & Calle 2003; Haugaasen & Peres 2005; Desbiez 2009). With wide-ranging behaviour and slow reproductive rates, tapir populations rarely reach a high local abundance. For these reasons, tapirs are particularly susceptible to habitat fragmentation. Population density is limited to the number of animals that a given area can support (Robinson & Redford 1986). Furthermore, while habitat fragmentation leads to small populations, further threats such as hunting, road-kill, and disease among others override the impact of fragmentation strongly impacting the likelihood of extirpation of remaining tapir populations (Bodmer *et al.* 1997; Cullen *et al.* 2000). Small tapir populations can show rapid decline and even local extinctions when affected by such threats (Medici *et al.* 2007a). The low rates of population growth, long generation time, long reproductive cycles, and delay in first reproduction are life-history characteristics that make tapirs particularly susceptible to overhunting (Bodmer *et al.* 1997). Lowland tapir populations showed rapid declines when overhunted in intact Amazonian forests in Peru (Bodmer *et al.* 1997). Peres (2000) predicted that the extinction rate of large terrestrial vertebrates is a function of fragment size in Amazonian forests, and is aggravated by hunting pressure. Cullen *et al.* (2000) compared the abundance of mammalian species in slightly and heavily hunted fragments of Atlantic Forest of the Interior - including Morro do Diabo State Park as one of the slightly hunted sites - and observed that tapirs could not cope with persistent hunting and were extirpated from heavily hunted sites.

The destruction and fragmentation of the Atlantic Forest of the Interior of the Pontal do Paranapanema Region is relatively recent when compared to areas in the eastern part of the biome. Despite the extensive loss of habitat, some of the larger forest fragments in the region, particularly Morro do Diabo, still host populations of several species of large mammals, including lowland tapirs. During a biodiversity assessment, all the forest fragments larger than 4 km^2 in the Pontal do Paranapanema Region were surveyed for flora and fauna (Ditt 2002). The presence of tapirs was confirmed in eight of these forest fragments, including Morro do Diabo and seven smaller forest fragments in its surroundings. Tapirs were absent in six forest fragments surveyed during the study, local extinctions that were most probably due to overhunting (Cullen 1997; Cullen *et al.* 2000). The estimate of the size of these remaining tapir populations in the Pontal do Paranapanema Region will allow for an evaluation of their current conservation status, and for the understanding of how tapirs have been affected by the past process of habitat fragmentation. In addition, this information will be vital for the evaluation of the potential impact of existing threats to tapirs in the region, and for the assessment of the viability of these tapir populations over the long-term. Finally, this information will be used to determine the tapir population parameters, most importantly population size and carrying capacity, for the process of Population Viability Analysis (PVA) presented in Chapter 6.

In this Chapter, I used different methodologies to estimate the size of tapir populations in the Atlantic Forest fragments in the Pontal do Paranapanema Region. Radio-telemetry, nocturnal line-transect sampling, and Footprint Identification Technique (FIT) were used to estimate tapir density in Morro do Diabo. Various methods of data analysis were used and one density estimate was selected as the most appropriate to derive tapir population sizes in Morro do Diabo and surrounding forest fragments. The advantages and disadvantages of each method, as well as their reliability for long-term tapir monitoring, are presented and discussed.

4.2 Methods

I used three methods to estimate tapir population density in Morro do Diabo:

- Radio-Telemetry
- Nocturnal Line-Transect Sampling
- Footprint Identification Technique (FIT)

4.2.1 Estimate of Tapir Population Density using Radio-Telemetry Data

Radio-telemetry has been extensively used to derive animal density, by providing data on home range size and home range overlap (Karanth 1995; Keuroghlian *et al.* 2004; Crawshaw 2004; Soisalo & Cavalcanti 2006). VHF telemetry was used to study tapir ranging behaviour in Morro do Diabo. A complete overview of the use of radio-telemetry as well as results of home range size, home range radius, and home range overlap obtained from 19 tapirs radio-tracked in Morro do Diabo for varying amounts of time have been presented in Chapter 3. Tapir home range size was calculated using Kernel Density Estimator (KDE95%) and Minimum Convex Polygon (MCP95%). Home range overlap was calculated by KDE95%.

I used four analytical methods based on different parameters of tapir ranging behaviour obtained by radio-telemetry to estimate tapir population density in Morro do Diabo. I was interested in evaluating the importance of different ranging parameters in estimating tapir density. The methods were the following:

Method 1 Tapir density was estimated by extrapolating mean tapir home range size obtained by both KDE95% (4.7 km^2) and MCP95% (4.4 km^2) to the entire area of 370 km^2 of Morro do Diabo. The density estimates obtained through this method did not consider home range overlap. For this analysis I used only the ranging results obtained from the 14 tapirs radio-tracked from 8-36 months.

Method 2 Tapir density was estimated by subtracting mean home range overlap (37%, KDE95%) from mean tapir home range size (4.7 km^2, KDE95%). The value obtained was then extrapolated to the entire area of 370 km^2 of Morro do Diabo to obtain a density estimate. Once more, for this analysis I used only the ranging results obtained from the 14 tapirs radio-tracked from 8-36 months.

Method 3 Tapir density was estimated as the number of radio-tracked tapirs (in this case, all 19 individuals monitored during the study in Morro do Diabo) divided by the total area which they used, known as the Effective Sampled Area (ESA).

ESA was estimated as the total area making up the tapir home ranges and was calculated through both KDE95% and MCP95% for comparison. The resulting density of tapirs in the ESA was then extrapolated to the entire area of 370 km² of Morro do Diabo to obtain a density estimate. Densities for females and males were estimated separately. This method of estimating density from radio-collared animals takes overlap between individuals into consideration (Crawshaw 1995; Burch 2001).

Method 4 Mean home range radius (½ Mean Maximum Distance Moved - MMDM) was calculated for the 14 tapirs radio-tracked from 8-36 months (Chapter 3). This value was used to determine the ESA by placing circular buffers around all locations where different tapirs were captured during the study (N=35 tapirs; N=14 capture sites) (Wilson & Anderson 1985; Karanth & Nichols 2002). The resulting density of tapirs in the ESA was then extrapolated to the entire area of 370 km² of Morro do Diabo to obtain a density estimate. Additionally, I calculated home range radius for females (N=20; N=11 capture sites) and males (N=15; N=9 capture sites) and estimated their densities separately. This method takes overlap between individuals into consideration (Wilson & Anderson 1985; Karanth & Nichols 2002).

4.2.2 Nocturnal Line-Transect Sampling

4.2.2.1 Line-Transect Sampling Methodology

Line-transect sampling is a convenient and relatively inexpensive technique (Buckland *et al.* 2001). It has been commonly used to estimate densities and abundance of large- and medium-sized Neotropical mammals (Bodmer *et al.* 1997; Chiarello 2000; Cullen *et al.* 2000; Mendes-Pontes 2004; Desbiez 2010).

Line-transect estimation of wildlife populations can be based on either right-angle distances or radial distances, and sighting angles to the detected objects (Hayes & Buckland 1983; Buckland *et al.* 2001). In the standard method, all objects (animals) on or near the line should be detected, but the method allows a proportion of objects to be missed. As the distance from the line increases, animals are harder to detect and more animals go undetected. The reliability of line-transects to estimate density depends largely on the sample size of observations (Burnham *et al.* 1980; Buckland *et al.* 1993; Wilson *et al.* 1996).

The principle behind line-transect sampling is to use the distribution of observed distances to estimate a "detection function", and then model the probability of detecting animals as a function of distance from the transect line. The estimation procedures are described in detail by Buckland *et al.* (2001). Other factors besides distance from the line, such as habitat type, experience of observer and weather conditions may affect the probability of detecting an animal along the line-transect (Burnham *et al.* 1980; Buckland *et al.* 2001; Buckland *et al.* 2004). In this study, line-transects were always carried out by the same observers, when it was not raining, and the habitats sampled were always forested.

Five assumptions are essential for reliable estimation of density from line-transect sampling, and every possible effort was made to ensure that these assumptions were not violated during this study:

- line-transects are located at random within the study area and are independent of animal distribution;
- animals directly on the line-transect are always detected (probability=1);
- animals are detected at their initial location, prior to any movement in response to the observer;
- distances and angles are measured accurately; and
- detections are independent events.

4.2.2.2 Line-Transect Sampling Data Collection

In July 2006, a total of eight line-transects from 6-7.7 km, and with an average length of 7,125 km, were selected within Morro do Diabo. Internal dirt roads distributed throughout the area of Morro do Diabo were used as transects (Figure 4.1). These same roads had been previously used for a diurnal census of terrestrial mammal species in Morro do Diabo during the 1990's (Cullen 1997; Cullen *et al.* 2000), which allowed for comparisons between diurnal and nocturnal line-transect sampling for tapirs. These roads were rarely used by the park staff and/or other researchers, and tapirs were initially assumed not to avoid or prefer these areas.

Data collection on transects was carried out over 20 months from August 2006 to March 2008. Transects were walked by two observers equipped with head-lights and a 60-watt hand-held spotlight. Observers walked slowly at ~1-2 km/h. Transects were censused between 18:00-23:00 h, but census was terminated during rain. The direction of travel was changed from start to end, from end to start, every two months. Date, time, GPS coordinates, radial distance from the line-transect, angle (azimuth) to the animal, and number of individuals were recorded for each tapir encounter. Tapirs either visualised or heard were recorded. Radial distances from the observer to the sighted/heard tapir were estimated to the nearest meter by counting steps. I also made general notes about sex, age class, behaviour, weather conditions, and phase of the moon. Each transect was walked once a month, completing a monthly census effort of 57 km, and a final total censusing effort of 1,140 km walked.

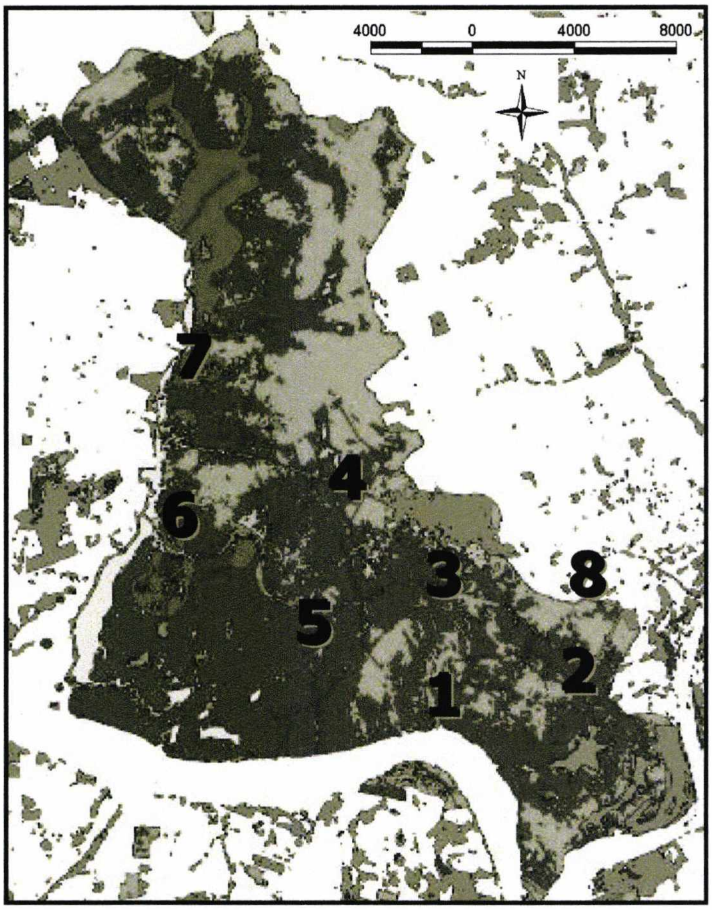


Figure 4.1. Locations of eight line-transects used for the lowland tapir nocturnal line-transect sampling in Morro do Diabo State Park, São Paulo, Brazil. (Transects: (1) Taquara, (2) Córrego Seco-Pinus, (3) Pinus-Linha de Trem, (4) 7000-3000, (5) Angelim, (6) Estreito de Baixo, (7) Caldeirão, and (8) Aeroporto). Figures 2.5 and 2.6 (Chapter 2) provide further reference on the location of Morro do Diabo State Park.

4.2.2.3 Estimate of Tapir Population Density using DISTANCE Analysis

Tapir density was analysed using DISTANCE 5.0 software (Buckland *et al.* 2001). DISTANCE is a Windows-based computer package that allows users to analyse line-transect sampling surveys and estimate densities of wildlife populations. As a first step, I carried out an exploratory analysis of the line-transect data using the DISTANCE's Data Filter in order to check for violation of assumptions. I plotted a histogram of frequency of tapir encounters against distance from the line-transect (Figure 4.2). Two problems were found. The first was a high frequency of encounters at zero distance. In line-transect sampling, it is common to find the highest frequency of animal sighting counts at zero distance or at distances near zero. However, this prevents the data from fitting the model. Normally, the frequency of animal sightings during the first few distance intervals should not be radically different since almost all animals at short distances from the line-transect should be detected. The histogram should present a "shoulder" at short distances before decreasing. The spike at zero distance illustrates a violation in the initial assumptions. The second problem relied on the fact that one of the line-transects was located along the southern border of Morro do Diabo and one of its sides was a crop field. On the side of this particular transect, I had a visibility of over 100 m and a number of tapirs were sighted within that range. Once I identified these problems, I established left truncation at distance 0.1 m and right truncation at 35 m (estimated maximum visibility for the forested environment of Morro do Diabo) and DISTANCE's Data Filter discarded all outliners.

The next step was the definition of the most appropriate model to fit the tapir line-transect data. A central part of the analysis of line-transect data is modelling of the detection function. DISTANCE's Model Definition options include the analysis engine to be used, the type of detection function model (Uniform, Half-Normal, Hazard-Rate and Negative Exponential), series expansions (Cosine, Simple Polynomial and Hermite Polynomial), and the method of estimating variance (analytic vs. bootstrap). I used the Conventional Distance Sampling (CDS) analysis engine as the data did not include any covariates. In the CDS engine, only one level of stratification is allowed (Buckland *et al.* 1993; Buckland *et al.* 2001). All possible combinations of detection function models (with exception of Negative Exponential) and series expansions were tested. The Akaike's Information Criterion (AIC) was used to select the combination that produced the best model fit. AIC is computed for each candidate model, and that with the lowest AIC is selected for analysis and inference. Model fit, the fit of the estimated detection functions to the empirical histograms of distance data, was assessed through the Qq-plot and the Chi-sq goodness-of-fit, Kolmogorov–Smirnov (k-s) and Cramér–von Mises (C-vM) tests reported by DISTANCE. Based on AIC and likelihood ratio tests, the Half-Normal detection function in combination with the Simple Polynomial series expansion was selected. Chi-sq goodness-of-fit, Kolmogorov–Smirnov (k-s) and Cramér–von Mises tests were insignificant, indicating good fit of the detection function model to the corresponding empirical frequency histogram of distance data. I used the analytic variance estimate.

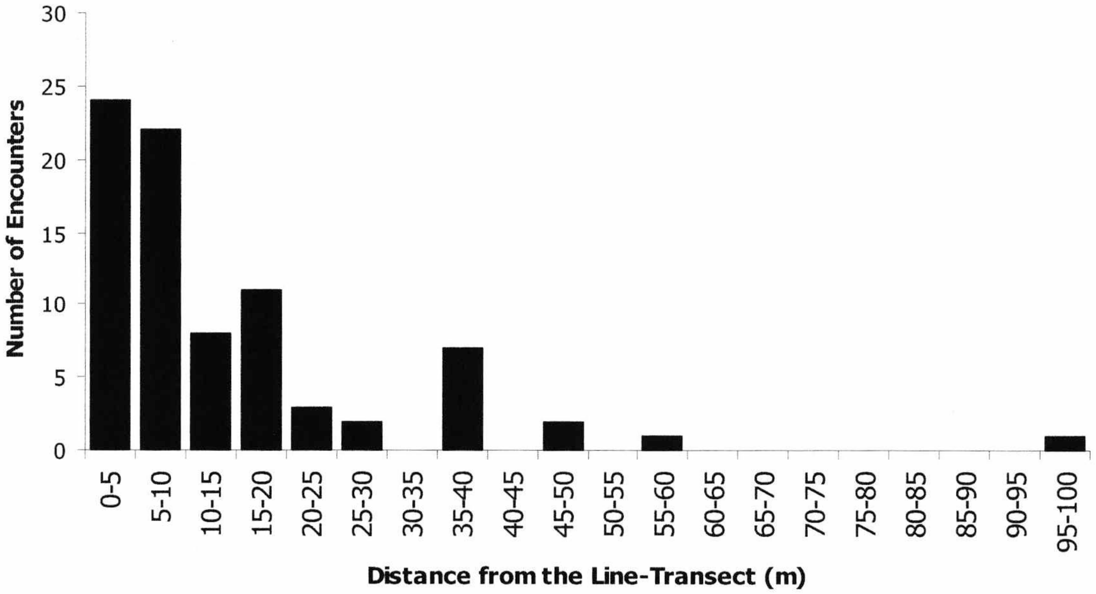


Figure 4.2. Histogram of frequency of lowland tapir encounters against distance from the transect (metres) during the nocturnal line-transect sampling in Morro do Diabo State Park, São Paulo, Brazil. The total number of tapir encounters was 81.

4.2.3 Footprint Identification Technique (FIT)

The Footprint Identification Technique (FIT) is a cost-effective and non-invasive research tool developed by WildTrack, an independent wildlife research group based in Portugal (Jewell *et al.* 2001; Alibhai *et al.* 2008). This method is an adaptation of ancient bushman tracking techniques to take advantage of the scientific objectivity modern technology can provide. The technique is based on the identification of animals at the species, individual, age-class and sex levels, using digital images of their footprints (Jewell *et al.* 2001; Alibhai *et al.* 2008).

4.2.3.1 Development of the FIT Algorithm for Lowland Tapirs

The first step in using FIT is to build a reference library of footprint images from a group of identifiable individuals of the species one is working with.

WildTrack has developed a very specific protocol to photograph animal footprints:

1) It is required to have a clear "track" (series of footprints of the same individual along a trail). A minimum of 15-20 left hind (LH) footprints from the same animal must be photographed (Figure 4.3.1).

2) Once the first footprint of the "track" is selected, it is necessary to place a cm ruler for scale on bottom and left hand axis of footprint, in relation to direction of travel. It is important to make sure the ruler does not obscure footprint detail at all. The same procedure is done for every footprint to be photographed (Figure 4.3.2).

3) A photo ID slip giving details of each footprint must be included in the photograph. The slip contains the date, name of photographer, and animal ID, as well as a footprint number that refers to the number allocated to the footprint for that day's work. The first LH footprint in the "track" is called 1A, the second 1B, the third 1C and so on. Footprints from a second "track" will be 2A, 2B and so on (Figure 4.3.2).

4) Photographs should be taken with a minimum 300KB image size, using 768X1024 resolution or higher. Camera lens should be directly overhead of the footprint, and fill the camera frame with the footprint, ruler and ID slip so that the photo is filled with details of spoor. It is important to try and get the best possible light contrast - usually found early morning and later afternoon, and avoiding casting shadow on the footprint (Figure 4.3.3).

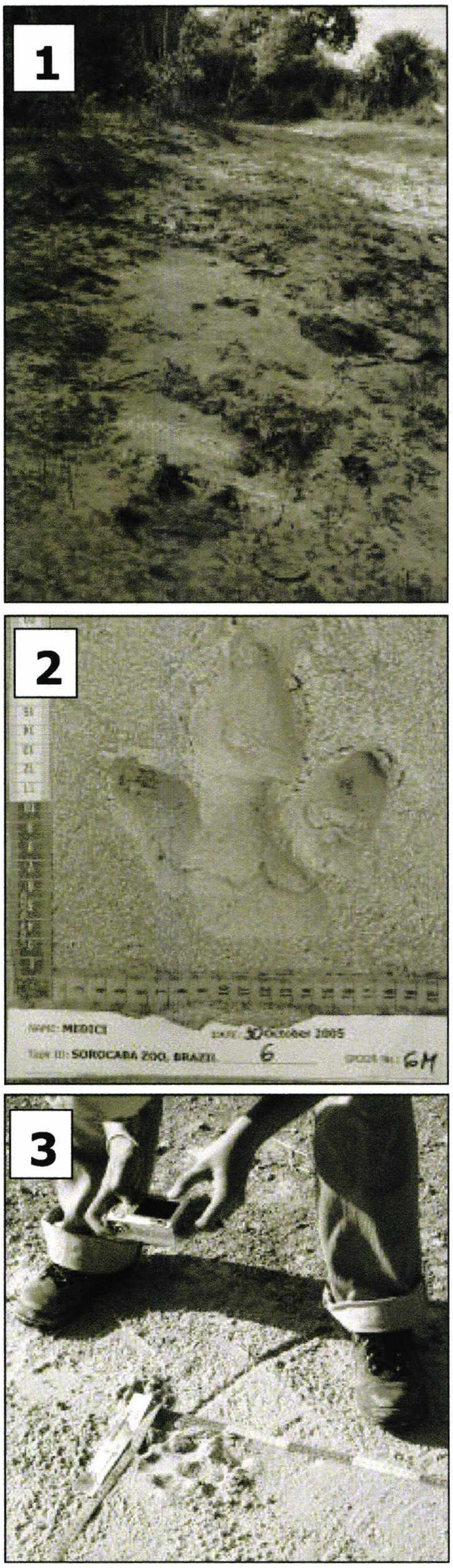


Figure 4.3. 1- Lowland tapir "track" along a dirt road; 2- Lowland tapir footprint prepared to be photographed (cm tape measures for scale on bottom and left hand axis of footprint, and photo ID slip providing details of the footprint); 3- Photography being taken. Photos by Patrícia Medici.

From April 2005 to April 2006, I organised the collection of sets of footprint images from 28 captive lowland tapirs (15 females and 13 males; all individuals of known age) from four zoological institutions and breeding facilities in Brazil and Argentina (Table 4.1). Additionally, I received contributions of additional footprint images from two zoos in France (Parc Zoologiqué Amnéville and Safari de Peaugres), one zoo in Colombia (Zoológico de Cali), and from tapir field researchers in Ecuador (Andrés Tapia) and French Guiana (Benoit de Thoisy). However, these additional datasets were too small to be included in the analysis.

Table 4.1. Zoological institutions and breeding facilities where captive lowland tapir footprint images were collected for the establishment of the initial reference library for Footprint Identification Technique (FIT). Number of photos taken and average number of footprints per track in each facility are shown. (N=number of tapirs; F=female; M=male).

Facility	N	Number of photos taken	Average number of footprints/set
Criadouro Conservacionista CBMM - Brazil	10 (5F/5M)	265	27
Criadouro Conservacionista Martins, Brazil	10 (7F/3M)	224	22
Sorocaba Zoo, Brazil	6 (2F/4M)	116	19
Fundación Temaikén, Argentina	2 (1F/1M)	21	10

All photographs were taken in fine sand substrate. At the Sorocaba Zoo, where I personally conducted the process of photographing the footprints, we carried large amounts of sand into the tapir exhibit and prepared a 1.5-m wide, 10-m long sand path. One by one, tapirs were lured with bananas and encouraged to walk over the sand path while we marked their left hind footprints. Each individual tapir had to be walked over the sand path twice so that I could obtain the minimum number of footprint images per animal. All photographs were taken in high resolution and I followed the WildTrack protocol very closely.

Our reference library of footprints of captive tapirs was then subjected to pre-processing and statistical analysis by WildTrack researchers aiming at developing an algorithm function for the identification of individual lowland tapirs. Pre-processing consisted of selecting the images to be included in the analysis and posterior image enhancement. From a total of 626 photographs taken, 362 confirmed left hind footprints were considered to be adequate for analysis. The best images were those where protocol had been followed closely.

The identification of an individual through FIT is based on the geometric profiles of its footprints. Therefore, the implementation of FIT to a new species requires the choice of a set of natural landmarks determined by the structure and complexity of the footprint. The forefeet of lowland tapirs have three main digits, and a smaller one, which only leaves an impression when the tapir is walking on soft ground. The hind feet have only three digits. All the toes are hoofed. The plantar cushion helps support the distal metatarsals and digits where they make ground contact (Figure 4.4.1). The impression made by the foot can reveal clear outlines of the outside edge of each hoof (Figure 4.4.2).

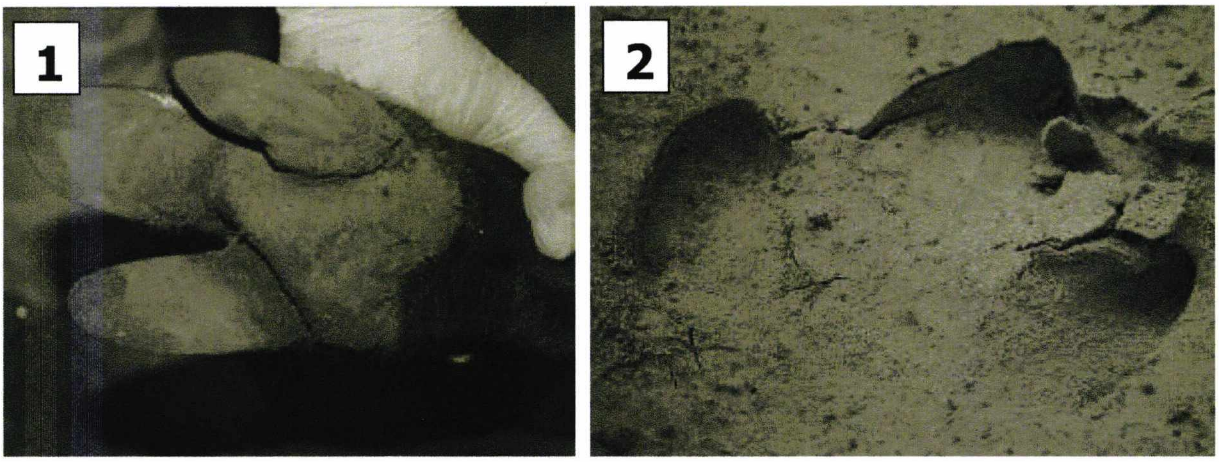


Figure 4.4. 1- Lowland tapir plantar cushion, distal metatarsals and digits; 2- Close up image of a left hind (LH) footprint of a lowland tapir in Morro do Diabo State Park, São Paulo, Brazil. Photos by Patrícia Medici and Joares May.

The natural landmark points are selected on the basis of foot anatomy to include those points, which are clearly definable and repeatable across many footprints. Footprint images are downloaded into a computer and landmark points are marked using an image processing computer package such as ADOBE PHOTOSHOP (Adobe Inc). After placing these landmark points, a set of derived landmarks, geometrically constructed from the set of natural landmarks, is then defined, including lengths and angles (variables). This set of measurements constitutes the geometric profile of the footprint image, and provides the data upon which all FIT analyses are performed (JMP Statistical Software).

The set of measurements typically contains many variables (90 in the case of the lowland tapir). The FIT analysis is based on 95% confidence interval ellipses around Reference Centroid Values (RCV) generated using two canonical variables for each "track" (each animal). The first step in constructing a specific FIT algorithm is the reduction of the set of measurements to the variables that will actually be used in FIT analyses. Using a stepwise technique, a reduced number of measurements with the highest F-ratios (optimum discrimination) are then selected (14 for lowland tapirs) for the generation of ellipses. The sets of footprints are then compared in a pair-wise interaction in the presence of the Reference Centroid Value (RCV) using those 14 variables in the algorithm. The presence or absence of overlap of the 95% confidence interval ellipses is used as the classifier. If two "tracks" belong to the same individual then the ellipses should overlap (Figure 4.5.1). With "tracks" from different individuals there should be an absence of overlap (Figure 4.5.2). The system is based on being able to accurately identify tracks with 6-8 footprints in the presence of a constant 'Reference Centroid Value' (Jewell *et al.* 2001; Alibhai *et al.* 2008).

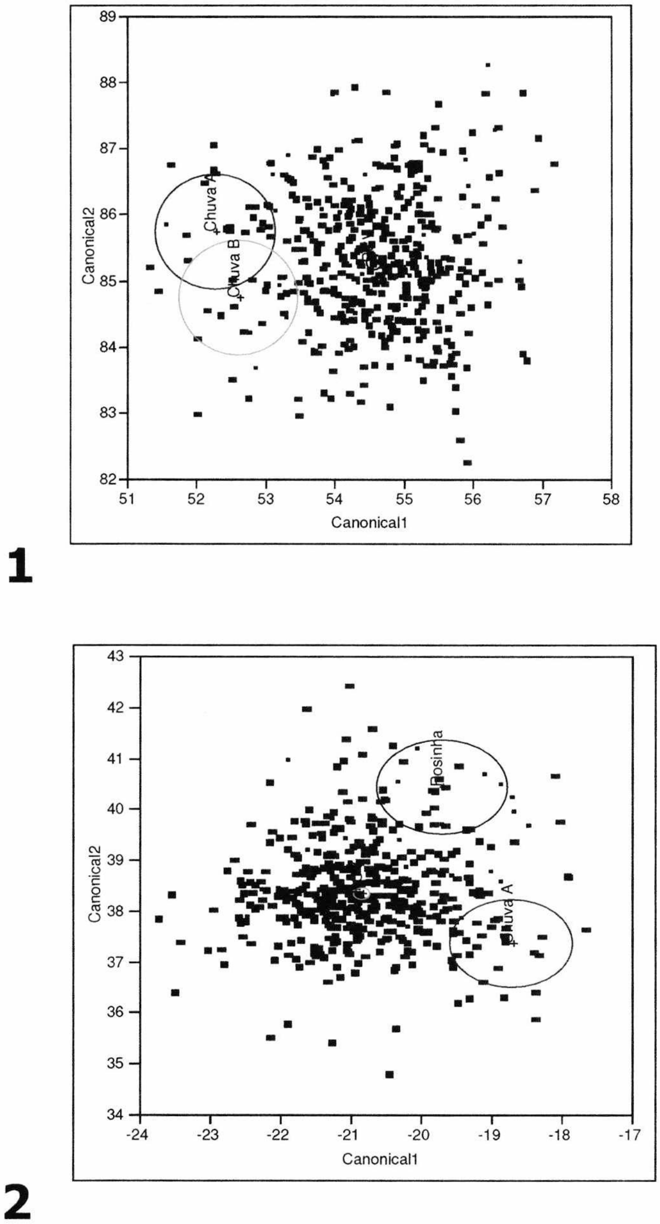


Figure 4.5. 1- Overlap of 95% confidence interval ellipses of 2 self tapir tracks (Chuva A and Chuva B, adult female) indicating correct identification; 2- Absence of overlap of ellipses of 2 non-self tapir tracks (Rosinha & Chuva A, both adult females) once again indicating correct identification and separation of different individuals.

The FIT algorithm function for lowland tapirs resulted in an overall accuracy of 97% that any one "track" could be identified correctly. The system was thus very accurate in discriminating different individuals. Besides developing an algorithm that could discriminate at the individual level, I wanted to determine gender and age of the tapirs. For this purpose, WildTrack researchers developed specific algorithms for sex and age class. Based on the age estimates provided for each captive tapir sampled, five age classes were established: A (0-1 year old), B (1.1-3), C (3.1-6), D (6.1-10), and E (10.1 and older). The accuracy for gender determination was 82% and for age determination 83%. It was not possible to validate the accuracy of age determination, since ages for some of the initial library animals were estimates. The Sorocaba Zoo and the two breeding facilities in Brazil did not have complete records of the ages of their tapirs as some of the animals were exchanges from other facilities and some were wild-born.

4.2.3.2 Validation of the FIT Algorithm for Lowland Tapirs

Once the initial algorithm was developed, its robustness was tested in two different ways. First, WildTrack researchers used verification footprints collected from wild tapirs for testing against the primary database and refining the algorithm. I collected six different sets of footprint images from unknown wild tapirs in Morro do Diabo (56 pictures taken, average of 9 footprints per set). These sets of footprint images were collected in areas of Morro do Diabo that were very far apart so I assumed with confidence that I was not photographing footprints of the same individual. Of these, only five sets were usable. Sets 2, 3 and 5 separated out completely from the others discriminating three different individuals. Sets 1 and 6 were very close to each other and they were both classified as females. However, their age classes were different enough to suggest that they came, in all likelihood, from different tapirs. The verification sets of footprints from wild tapirs were consistent with the main database in their characteristics. The initial algorithm appeared to be robust and adaptable for wild tapirs.

The second step on the process of testing the robustness of the algorithm was to build on the main database with some larger sets of footprints from known captive tapirs. WildTrack researchers wanted to have a few databases of captive tapirs with 30 footprints per set so that these sets could be split up into small clusters of footprints from the same animal and tested against themselves in order to finalise the validation of the algorithm.

In August 2006, I went back to the Sorocaba Zoo and collected sets of footprint images from four of the tapirs I had photographed previously (2 females and 2 males). I took an average of 17 footprints per animal, which enlarged the databases of those four tapirs considerably. Additionally, in January 2007, I collected sets of footprints from two captive lowland tapirs (2 males) from the Houston Zoo Inc. in the United States (60 photos taken - 30 footprints per set). With this, we had six samples (tapirs) with databases equal or larger than 30 footprints. Analyses of comparison of clusters of the same animal were carried out, the algorithm was adjusted and indeed continued to present high accuracy in discriminating between individuals. After this final step, the algorithm was finalised and the Footprint Identification Technique for lowland tapirs was ready to be applied in the field.

4.2.3.3 Estimate of Tapir Population Density using FIT

From February to April 2007, I collected 27 sets of left hind (LH) footprint images from wild lowland tapirs along two internal roads in the central area of Morro do Diabo. The total length of transect surveyed was 11,535 m (road 1 = 6,400 m; road 2 = 5,135 m). The soil in Morro do Diabo is very sandy, which is a perfect substrate for finding and photographing tapir footprints.

A total of 393 photos were taken, with an average of 15 footprint images per set. The maximum number of footprint images per set was 27 and the minimum was 4. Once again, all photographs were taken in high resolution and following the WildTrack protocol very closely. The coordinates of every set of footprints photographed was recorded with a GPS. Only fresh prints were photographed. We avoided the risk of collecting a footprint more than once by obliterating each footprint after photography. WildTrack researchers processed and analysed the 27 sets of footprints and determined the number of different individual tapirs identified through FIT analysis, as well as their gender and age classes.

In order to calculate the Effective Sampled Area (ESA) where the FIT tapir population size (N) was estimated, I used an approximation of the method applied for camera-trap studies. In camera-trap studies, the ESA is determined by placing a buffer, equal to ½ the Mean Maximum Distance Moved (½MMDM) of all 'recaptured' animals, around the entire camera trapping grid, or around each camera station (Karanth 1995). Because most camera studies lack data on the target animal's home-range, the ½MMDM buffer is used as a proxy for home range radius (Wilson & Anderson 1985; Karanth & Nichols 2002).

I calculated Maximum Distance Moved (MDM) using different types of data and three analytical methods. I was interested to evaluate most appropriate way to establish Effective Sampled Area (ESA) for FIT analysis. The methods were the following:

Method 1	I used the dataset of FIT footprint photos to calculate the Mean Maximum Distance Moved (MMDM) among locations where the same individual tapir had its footprints photographed. The MDM was calculated by plotting the GPS coordinates of photos of the footprints of the same individual tapir in the software TRACKER1.1 (Camponotus Radio Location Systems AB 1994).
Method 2	I used radio-telemetry results to calculate the Mean Maximum Distance Moved (MMDM) by 7 tapirs (5 females and 2 males) radio-tracked in the Centre of Morro do Diabo, where FIT was applied. The MDM for each radio-tracked tapir was calculated through analysis of their home-ranges estimated by MCP95% in the software TRACKER1.1.
Method 3	I used data on locations of tapir capture sites to calculate the Mean Maximum Distance Moved (MMDM) among traps where the same individual tapirs had been re-captured during the study. For this analysis, I included 17 tapirs (11 females and 6 males) captured and re-captured in five wooden corrals in the centre of Morro do Diabo, where FIT was applied. The MDM was calculated by plotting the GPS coordinates of tapir capture and re-capture sites in the software TRACKER1.1.

The results of Mean Maximum Distance Moved (MMDM) were used to calculate three different values of home range radius (½MMDM), which were then used to establish a buffer around the total length of the two roads sampled for FIT and calculate Effective Sampled Area (ESA). Three different results of ESA where the FIT tapir population size (N) was determined were obtained. The resulting densities of tapirs in the calculated ESAs were then extrapolated to the entire area of 370 km^2 of Morro do Diabo, and three different density estimates were obtained.

4.2.4 Estimates of Lowland Tapir Population Size

I selected one density estimate as the most appropriate from among those estimated for this study, and used it to derive tapir population sizes in Morro do Diabo and surrounding forest fragments where the presence of tapirs had been previously confirmed (Ditt 2002).

4.2.5 Comparisons between Density Estimators

I compared the three density estimators used during the study through paired ranking according to a selected set of criteria including: (i) cost, (ii) requirement of personnel, and (iii) field effort.

4.3 Results

4.3.1 Estimate of Tapir Population Density using Radio-Telemetry Data

The radio-telemetry density estimates were carried out using four analytical methods that generated six different density results that varied from 0.21 tapirs km^{-2} to 0.43 tapirs km^{-2}. For ease of reference, estimates of tapir population size derived from all radio-telemetry estimates of tapir density in Morro do Diabo are presented in Table 4.2.

Method 1 - Tapir density was calculated through extrapolating mean tapir home range size to the entire area of 370 km^2 of Morro do Diabo. This produced an estimate of 0.21 tapirs km^{-2} when using KDE95%, and 0.23 tapirs km^{-2} when using MCP95%.

Method 2 - Tapir density was based on subtracting mean home range overlap of 37% (KDE95%) from the mean tapir home range size of 4.7 km^2 (KDE95%) and extrapolating the obtained value to the entire area of 370 km^2 of Morro do Diabo. This produced an estimate of 0.34 tapirs km^{-2}.

Method 3 - Tapir density was based on the number of radio-tracked tapirs (N=19) divided by the total area which they used, known as the Effective Sampled Area (ESA), and extrapolating the obtained value to the entire area of 370 km^2 of Morro do Diabo. This produced an estimate of 0.33 tapirs km^{-2} when using KDE95%, and 0.43 tapirs km^{-2} when using MCP95%. Density estimates for both sexes resulted in estimates of 0.31 females km^{-2} and 0.21 males km^{-2} when using KDE95%, and 0.38 females km^{-2} and 0.26 males km^{-2} when using MCP95%.

Method 4 - Tapir density was based on estimating home range radius and placement of circular buffers around locations of tapir capture sites using the ESA, and extrapolating the obtained value to the entire area of 370 km^2 of Morro do Diabo. This produced an estimate of 0.32 tapirs km^{-2}. Density estimates for both sexes resulted in estimates of 0.27 females km^{-2} and 0.12 males km^{-2}.

Table 4.2. Estimates of lowland tapir density (tapirs km^{-2}) in Morro do Diabo State Park, São Paulo, Brazil, using radio-telemetry data. Four different analytical methods were applied. Home range size (km^{2}), home range overlap, Effective Sampled Area (km^{2}), and home range radius (m) used for different density estimates, as well as estimates of population size are shown. (N=number of tapirs; F=female; M=male; KDE=Kernel Density Estimator; MCP=Minimum Convex Polygon; NA=not applicable).

		Home Range Size (km^{2})	**Overlap**	**ESA** (km^{2})	**Density Estimate** (tapirs km^{-2})	**Population Size**
Method 1	**KDE95%** (N=14)	**4.7**	Not considered	NA	**0.21**	**79**
	MCP95% (N=14)	**4.4**	Not considered	NA	**0.23**	**85**
Method 2	**KDE95%** (N=14)	**4.7**	**37%**	NA	**0.34**	**126**
Method 3	**KDE95%** (N=19)	NA	Considered	57.7	**0.33**	**122**
	F (N=13)	NA	Considered	42.3	0.31 females km^{-2}	114 females
	M (N=6)	NA	Considered	28.6	0.21 males km^{-2}	78 males
	MCP95% (N=19)	NA	Considered	44.3	**0.43**	**159**
	F (N=13)	NA	Considered	34.0	0.38 females km^{-2}	142 females
	M (N=6)	NA	Considered	22.9	0.26 males km^{-2}	97 males
Method 4	**All captured tapirs** (N=35) 14 capture sites	NA	Considered	111 (½MMDM = 1,616 m)	**0.32**	**118**
	All captured F (N=20) 11 capture sites	NA	Considered	73 (½MMDM = 1,516 m)	0.27 females km^{-2}	101 females
	All captured M (N=15) 9 capture sites	NA	Considered	121 (½MMDM = 1,834 m)	0.12 males km^{-2}	44 males

4.3.2 Estimate of Tapir Population Density using Nocturnal Line-Transect Sampling

I recorded 81 tapir encounters while walking 1,140 km over 20 months of nocturnal line-transect tapir censusing in Morro do Diabo. Fifty-two of the encounters (64%) were actual sightings, and tapirs were heard in 29 occasions (36%). This was equivalent to an average of 4 encounters per month, and 0.1 tapir encounters per km walked. Put another way, it was necessary to walk 14 km to record a tapir encounter. Forty-one of the encounters took place in the wet season, and 40 during the dry season.

Most encounters (78%) were of solitary individuals, while 12% of the encounters were of pairs of tapirs (adult female with adult male or adult female with offspring). In 9% of the encounters, I could not determine the number of tapirs. On one occasion (1%), three tapirs were sighted. Tapir encounters took place from 18:42-21:31 h. Most encounters (47%) took place from 20:00-21:00 h, which coincides with the main peak of tapir activity calculated through radio-telemetry (Chapter 5). Most encounters occurred during the darker phases of the moon: 47% during the waning crescent, 21% during the new moon, 18% during the waxing crescent, and only 14% during the full moon.

The density of tapirs estimated by nocturnal line-transect sampling was 1.35 tapirs km^{-2}. Based on a 95% confidence interval, the minimum density was 0.64 tapirs km^{-2}, and the maximum was 2.86 tapirs km^{-2}. For ease of reference, estimates of tapir population size derived from line-transect sampling estimates of tapir density in Morro do Diabo are presented in Table 4.3.

Table 4.3. Estimates of lowland tapir density (tapirs km^{-2}) in Morro do Diabo State Park, São Paulo, Brazil, using nocturnal line-transect sampling. Standard error (SE), coefficient of variation (%CV), 95% confidence interval (95%CI), and estimates of population size are shown.

Density Estimate (tapirs km^{-2})	**SE**	**% CV**	**95% CI** (tapirs km^{-2})	**Population Size**
1.35	0.454	33.69	0.64-2.86	237-**499**-1058

4.3.3 Estimate of Tapir Population Density using Footprint Identification Technique (FIT)

4.3.3.1 FIT Identification of Individual Tapirs

The analyses of the 27 sets of footprint images from tapirs in the centre of Morro do Diabo identified 13 different individuals in the sample. Gender wise, these included 10 females and 3 males. Age wise, identified animals included 1 individual in category A (0-1 year old), 6 in category C (3.1-6), 1 in D (6.1-10), and 4 in E (10.1+). Tapir #1 could not be discriminated between categories C and D (Table 4.4). Because the analytical methods employed were deterministic rather than stochastic, it was not possible to attach confidence intervals to the figures. The accuracy of correct classification was over 90%.

With regard to relatedness of "tracks" (sets of footprints), while 11 tapirs were represented by either one or two tracks, Tapir #7 (female) was represented by 8 tracks and Tapir #10 (male) was represented by 5 tracks. This could be an indicative that Tapirs #7 and #10 could be the main reproductive pair in the sampled area in the centre of Morro do Diabo. Another indicative of social organisation was the fact that Tapir #4, a juvenile male (predicted age ≤12 months), had its tracks (Tracks 4 and 22) in close association with the tracks of Tapir #3 (Tracks 3 and 21), an adult female. The classification of Tapir #4 as a juvenile is very accurate given that age class A (≤12 months) ellipse in a two-way canonical plot separates out very clearly from the rest of the age classes. Looking at the footprint collection dates, it is noticeable that the images for adult female Tapir #3 were collected on the same dates as those of the juvenile Tapir #4. Moreover, the track numbers are in sequence *i.e.* Track 3 (mother) & Track 4 (calf), and Track 21 (mother) & Track 22 (calf) (Table 4.4).

Table 4.4. Relatedness of the 27 sets of footprints of wild lowland tapirs in Morro de Diabo State Park, São Paulo, Brazil, determined by FIT. The gender/age classes were established independent of track relatedness. For Tapir #1 the age class could not be separated out to a single category. Age classes were: A (0-1 year), B (1.1-3), C (3.1-6), D (6.1-10), and E (10.1+).

Tapir ID	Footprint Set # & Relatedness	Date of Collection	Gender	Age Class
1	**01**	28 February 2007	Female	C/D
2	**02** **05**	28 February 2007 28 February 2007	Female	D
3	**03** **21**	28 February 2007 10 April 2007	Female	C
4	**04** **22**	28 February 2007 10 April 2007	Male	A
5	**06**	28 February 2007	Male	C
6	**07**	28 February 2007	Female	E
7	**08** **09** **14** **15** **16** **18** **19** **27**	01 March 2007 01 March 2007 03 April 2007 03 April 2007 03 April 2007 03 April 2007 03 April 2007 10 April 2007	Female	E
8	**10**	01 March 2007	Female	C
9	**11**	01 March 2007	Female	E
10	**12** **13** **17** **23** **26**	01 March 2007 01 March 2007 03 April 2007 10 April 2007 10 April 2007	Male	C
11	**20**	10 April 2007	Female	C
12	**24**	10 April 2007	Female	E
13	**25**	10 April 2007	Female	C

4.3.3.2 Estimate of Tapir Population Density using FIT

The FIT density estimates were carried out using three different analytical methods, resulting that generated three different results that varied from 0.26 tapirs km^{-2} to 0.43 tapirs km^{-2}. For ease of reference, all estimates of tapir population size derived from FIT estimates of tapir density in Morro do Diabo are presented in Table 4.5.

Method 1 was based on calculating MMDM in between locations where the same individual tapir had its footprints photographed through FIT. This method resulted in a home range radius of 1,091 m (ESA=30 km^2) and a tapir density of 0.43 tapirs km^{-2}. Density estimates for both sexes resulted in estimates of 0.33 females km^{-2} and 0.10 males km^{-2}.

Method 2 was based on calculating MMDM within the home ranges of seven tapirs radio-tracked in the centre of Morro do Diabo. This method resulted in a home range radius of 1,672 m (ESA=50 km^2) and a tapir density of 0.26 tapirs km^{-2}. Density estimates for both sexes resulted in estimates of 0.20 females km^{-2} and 0.06 males km^{-2}.

Method 3 was based on calculating MMDM among traps where the same individual tapirs had been re-captured during the study. This resulted in a home range radius of 1,270 m (ESA=36 km^2) and a tapir density of 0.36 tapirs km^{-2}. Density estimates for both sexes resulted in estimates of 0.28 females km^{-2} and 0.08 males km^{-2}.

Table 4.5. Estimates of lowland tapir density (tapirs km^{-2}) in Morro do Diabo State Park, São Paulo, Brazil, using FIT data. Four different analytical methods were applied. Values of ½MMDM - Mean Maximum Distance Moved (home range radius, in m) and ESA - Effective Sampled Area (km^2) used for different density estimates, as well as estimates of population size are shown. (N=number of tapirs; F=female; M=male).

		½MMDM (m)	**ESA** (km^2)	**Density Estimate** (tapirs km^{-2})	**Population Size**
Method 1	**Tapirs Footprinted**	1,091	30	**0.43**	**159**
	F (N=10)			0.33 females km^{-2}	122 females
	M (N=3)			0.10 males km^{-2}	37 males
Method 2	**Radio-tracked Tapirs**	1,672	50	**0.26**	**96**
	F (N=10)			0.20 females km^{-2}	74 females
	M (N=3)			0.06 males km^{-2}	22 males
Method 3	**Traps/Recaptures**	1,270	36	**0.36**	**133**
	F (N=10)			0.28 females km^{-2}	103 females
	M (N=3)			0.08 males km^{-2}	31 males

4.3.4 Estimate of Lowland Tapir Population Sizes in Morro do Diabo State Park and Surrounding Atlantic Forest Fragments of the Pontal do Paranapanema Region

The lowland tapir densities estimated by radio-telemetry, nocturnal line-transect sampling, and Footprint Identification Technique (FIT) varied from 0.21 tapirs km^{-2} to 1.35 tapirs km^{-2}. I selected one of the density estimates (radio-telemetry Method 2, 0.34 tapirs km^{-2}), as the most appropriate within the study for estimating population size. This estimate was selected based on two main reasons. First, it incorporated the mean home range size of 4.7 km^{2} and mean home range overlap of 37% calculated for the 14 tapirs radio-tracked from 8-36 months. Thus, this estimate was strongly based on the ranging parameters of tapirs whose home ranges had reached asymptotes during their periods of monitoring. Second, this estimate was based on home range size and home range overlap calculated by Kernel Density Estimator (KDE). KDE is widely viewed as the most reliable method of home range estimate in ecology (Powell 2000; Kernohan *et al.* 2001; Hemson *et al.* 2005).

Therefore, I used this radio-telemetry density estimate to derive tapir population sizes in Morro do Diabo and seven other forest fragments where the presence of tapirs had been previously confirmed (Ditt 2002) (Figure 4.6). According to the selected density, there were 126 tapirs in Morro do Diabo and ~22 additional individuals distributed in the seven forest fragments. This resulted in a total number of ~148 tapirs in the entire Pontal do Paranapanema Region.

For reference, I also selected one tapir density calculated by nocturnal line-transect and one calculated by FIT for the estimate of tapir population sizes. The overall tapir density estimate obtained through line-transect (1.35 tapirs km^{-2}) was considered to be overly high. I decided to be conservative and selected the lower value of the DISTANCE 95%CI (0.64 tapirs km^{-2}) as a tolerable, although still very high, tapir density for the area. The resulting estimates were 237 tapirs in Morro do Diabo and 40 in the fragments, resulting in a total of ~277 tapirs in the entire Pontal do Paranapanema Region. Among the estimates obtained by FIT, I selected the one calculated through Method 1 (0.43 tapirs km^{-2}). Although high, this was the only FIT estimate totally based on the FIT's dataset of footprints, which could therefore allow for a full assessment of the effectiveness of the use of this technique without the support of other data. The resulting estimates were 159 tapirs in Morro do Diabo and 27 tapirs in the fragments, resulting in a total of ~186 tapirs in the entire Pontal do Paranapanema Region.

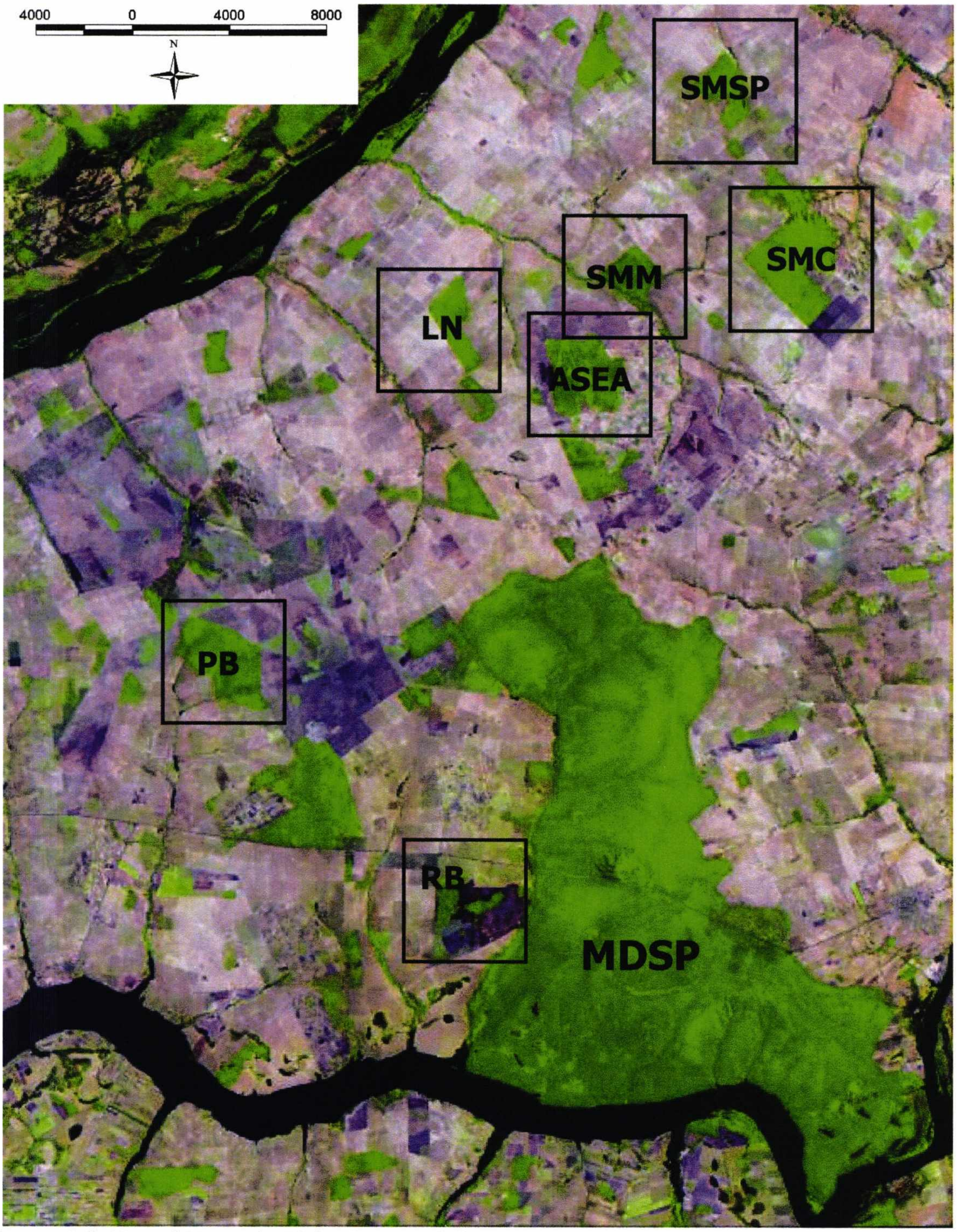


Figure 4.6. Map of Morro do Diabo State Park (MDSP) and seven surrounding forest fragments in the Pontal do Paranapanema Region, São Paulo, Brazil, where the presence of tapirs was confirmed (Ditt 2002). (MDSP: Morro do Diabo State Park; SMC: Santa Maria/Cachoeirinha; PB: Ponte Branca; ASEA: Água Sumida/Estrela da Alcídia; LN; Lua Nova/Santa Tereza da Água Sumida; SMM: Santa Maria dos Micos; SMSP: Santa Mônica/São Paulo; RB: Ribeirão Bonito). Note: SMC, ASEA, and PB are three of the four forest fragments encompassed by the Black-Lion-Tamarin Ecological Station. Figures 2.5 and 2.6 (Chapter 2) provide further reference on the location of Morro do Diabo State Park.

Table 4.6. Estimates of lowland tapir population size in Morro do Diabo State Park (MDSP) and seven surrounding forest fragments in the Pontal do Paranapanema Region, São Paulo, Brazil, where the presence of tapirs was confirmed (Ditt 2002). Density estimates were obtained by radio-telemetry, nocturnal line-transect sampling, and Footprint Identification Technique (FIT).

		Population Size (number of individuals)		
MDSP & Forest Fragments	**Area** (km^{2})	**Radio-Telemetry** 0.34 tapirs km^{-2}	**FIT** 0.43 tapirs km^{-2}	**Line-Transect** 0.64 tapirs km^{-2}
Morro do Diabo State Park (MDSP)	**370**	**126**	**159**	**237**
Santa Maria/Cachoeirinha (SMC)	18.3	6	8	12
Ponte Branca (PB)	13.0	4	6	8
Água Sumida/Estrela da Alcídia (ASEA)	12.1	4	5	8
Lua Nova/Santa Tereza da Água Sumida (LN)	5.4	2	2	3
Santa Maria Micos (SMM)	5.1	2	2	3
Santa Mônica/São Paulo (SMSP)	4.9	2	2	3
Ribeirão Bonito (RB)	4.2	2	2	3
Total number of Tapirs in Forest Fragments		**22**	**27**	**40**
Total number of Tapirs in the Pontal do Paranapanema Region (MDSP + fragments)		**148**	**186**	**277**

4.3.5 Comparison between Density Estimators

The three density estimators - radio-telemetry, nocturnal line-transect sampling, and Footprint Identification Technique (FIT) - were compared against each other based on the following criteria: (i) cost, (ii) requirement of personnel, and (iii) field effort (Table 4.7). It is important to note that the costs considered here involved only the implementation of the density estimators in the field, but excluded costs associated with data analysis.

Paired ranking resulted in the lowest score (0) for radio-telemetry. Radio-telemetry is by far the most expensive method, it requires large, multidisciplinary field teams for the different phases of the process (captures and monitoring among others), and its application requires a considerable field effort. Nocturnal line-transect sampling received a medium score (3). While this method does not require large field teams, it is relatively expensive as it requires extended periods of data collection in order to obtain the minimum number of sightings for DISTANCE analysis. FIT received the highest score (6). This method is inexpensive, it does not demand more than one or two team members for its application in the field, and it does not require large amounts of field effort.

Table 4.7. Paired ranking score of the three density estimators (radio-telemetry, nocturnal line-transect sampling, and Footprint Identification Technique) used during the lowland tapir study in Morro do Diabo State Park, São Paulo, Brazil. The criteria for ranking included cost, personnel, and field effort.

Density Estimator	Cost	Personnel	Field Effort	Score
Radio-Telemetry	High	High	High	**0**
Nocturnal Line-Transect Sampling	Medium	Low	Medium	**3**
Footprint Identification Technique (FIT)	Low	Low	Low	**6**

4.4 Discussion

4.4.1 Methodological Considerations on the Estimate of Tapir Population Size

Making accurate estimates of animal population size is very complex. Direct counts of animal populations are exceptionally difficult, if not impossible, to obtain. Animals are frequently difficult to capture or observe, and the associated costs and effort of making absolute counts are often prohibitive (Gittleman 1996). Thus, animal ecologists have no other alternative but to rely on indirect methods that provide indices of population abundance that are then applied to derive or estimate population size.

When selecting methods for estimating animal density, animal ecologists must be cautious to weigh the advantages and disadvantages of available methods and to make appropriate choices based on the circumstances in which they are working. The choice of a technique must consider the characteristics of the species being studied, the aim of the census, the degree of accuracy required, the costs involved, as well as the features of the environment (Caughley 1977; Seber 1973; Burnham *et al.* 1980; Riney 1982). Previous studies on lowland tapirs have applied a number of different methods to estimate population density including: radio-telemetry, diurnal and nocturnal line-transect sampling, and camera-trapping (Chapter 2, Table 2.7 provides a compilation of density estimates and bibliographical references). While methods of estimating animal population density have received considerable theoretical attention (Burnham *et al.* 1980; Clarke 1986; Pollock & Kendall 1987; Norton-Griffiths 1988; Buckland *et al.* 1993; Campbell & Borner 1995), empirical comparisons of methods have been less rehearsed (White *et al.* 1989; Bergstedt & Anderson 1990; Pojar *et al.* 1995; Noss *et al.* 2003; Soisalo & Cavalcanti 2006; Trolle *et al.* 2007; Dillon & Kelly 2008). Noss *et al.* (2003) used radio-telemetry simultaneously with camera-traps to estimate lowland tapir ranging parameters and population density in Kaa-Iya del Gran Chaco National Park, Bolivia. Trolle *et al.* (2007) used camera-trapping and diurnal line-transect sampling to estimate tapir density in a site of the Brazilian Pantanal. Nevertheless, to my knowledge, this long-term study in Morro do Diabo is the only one to date where three different methods to estimate population density - radio-telemetry, nocturnal line-transect sampling and Footprint Identification Technique - were used simultaneously on the same population.

4.4.1.1 Comparing Density Estimators: Cost, Personnel, and Field Effort

When comparing the three density estimators using the criteria of cost, requirement of personnel, and demand for field effort, radio-telemetry received the lowest score. Radio-telemetry was, without any doubt, the most expensive of all three methods. The use of radio-telemetry requires the purchase of very expensive pieces of equipment, large, multidisciplinary field teams, and considerable field effort. In terms of equipment, the purchase of 10 VHF radio-collars, one telemetry receiver, and a directional antenna for a telemetry study can easily cost over US$5,000. The costs escalate if GPS telemetry technology is used. Nowadays, a simple store-on-board GPS collar equipped with a VHF beacon and a drop-off component costs over US$3,000. In addition, the use of radio-telemetry requires the purchase of all the equipment and supplies necessary for the capture and immobilisation of the animals. These include a multitude of different items such as materials for trap construction, capture equipment such as CO_2 rifles and pistols, CO_2 cartridges, blow-pipes, darts, telemetry transmitters for darts (highly recommended when using the dart shooting capture method), drugs for chemical restraint (anaesthetics, reversal drugs, safety drugs among others), and all the veterinary gear for anaesthesia monitoring. The cost to build one wooden corral trap can be as high as US$850, including materials (wood, nails, rope, wire mesh among others), transportation of materials to the study site, and stipends for the personnel involved in the construction (usually 3-4 people). The cost of immobilising one individual tapir, including only the drugs can be as high as US$500. If the researcher chooses to take advantage of having an anaesthetised animal on his/her hands to collect samples of biological materials for epidemiological and genetic studies - which is strongly recommended given the urgent need for these types of information on tapirs - then an assortment of different types of materials for the collection, processing and storage of the samples is necessary.

An important factor that must be considered relies on the fact that most of the companies that manufacture reliable telemetry and capture equipment are based in the United States or Europe, usually far away from the countries where field research is being carried out. As a consequence, in order to purchase the equipment they need, researchers have to go through the process of importing the equipment, which almost always proves to be bureaucratic, time-consuming and expensive. In addition, in the case of equipment failure the malfunctioning item has to be sent back to the international company for repair, which incurs in more time lost and expenses.

Overall, the use of radio-telemetry demands considerable field effort on the part of the research team, particularly if using VHF telemetry, which requires radio-tracking animals. The results of this long-term telemetry study in Morro do Diabo showed that a minimum of 20 months of data collection is necessary to determine home range size for adult tapirs. For sub-adults, 32 months are needed. In addition, it is necessary to radio-track a large number of tapirs to have an adequate dataset to precisely estimate home range overlap, another important parameter for the estimate of population size. Radio-tracking a large number of different individuals for long periods of time can be very demanding. Thus, another significant cost that must be considered when budgeting for a tapir telemetry study is transportation.

During this study in Morro do Diabo, I radio-tracked tapirs mostly by car and the monthly expenses with fuel and car maintenance were considerably high. Sometimes airplanes are required for radio-tracking tapirs in remote areas.

In terms of personnel, the use of radio-telemetry requires large, multidisciplinary field teams for the different phases of the process. A minimum of three people is needed to build a corral trap. The construction of a pitfall trap requires 4-5 people. More importantly, the capture process requires the presence of at least one wildlife veterinarian to be in charge of immobilising animals, monitoring anaesthesia, and performing other procedures such as collection of biological samples. Forty-four tapir immobilisations and manipulations were carried out during this long-term study in Morro do Diabo, and the chemical restraint of free-ranging tapirs proved to be challenging. The involvement of a veterinarian who can select a safe anaesthetic protocol and carefully monitor the animals during anaesthesia will significantly reduce intrinsic risks of the capture process. Veterinarians are the only professionals qualified to quickly identify anaesthetic depression and take the appropriate measures. Thus, any researcher planning on capturing and immobilising tapirs in the wild must budget for a stipend for a well-experienced wildlife veterinarian.

Nocturnal line-transect sampling received a medium score. Neither large field teams nor a lot of equipment are necessary for the application of this method. Two people equipped with headlamps, a spotlight, a compass and a notepad can carry out the census. However, extended periods of data collection are needed in order to obtain the minimum number of observations required for DISTANCE analysis. For the study in Morro do Diabo it was necessary to accumulate 20 months of data collection and 1,140 km walked in order to obtain the minimum number of sightings. This was a considerable field effort and incurred in substantial expenses including stipends for the personnel involved as well as costs of transportation to and from the field site for 8 nights per month. There is also the danger of working at night.

The Footprint Identification Technique (FIT) received the highest score. This method is fairly inexpensive when compared to the others. The only pieces of equipment required for the application of FIT in the field are a good digital camera capable of taking high resolution pictures, a GPS unit, two rulers and a notepad, which are more often than not already available in most research programmes. The expenses involved in the use of FIT in the field included mostly the costs of transportation to and from the field site once a week. In addition, FIT does not demand more than 1-2 people for data collection. Furthermore, FIT does not require large amounts of field work. In Morro do Diabo, it was possible to walk through the entire length of the sampled roads and photograph as many as 5-7 different sets of tapir footprints in a single morning. However, the FIT sampling in Morro do Diabo was carried out for only three months and the results indicate that it would have been advisable to continue sampling for a longer period of time. It would have increased the probability of photographing and identifying all the different tapir individuals in the sampling area. However, even if I had increased the FIT sampling in Morro do Diabo, there would be still a smaller demand of field work when compared to nocturnal line-transect sampling and radio-telemetry.

Nonetheless, while the actual use of FIT in the field was inexpensive, practical and very straight forward, a great deal of time and financial resources were necessary to develop and validate the FIT algorithm for lowland tapirs until it was ready to be applied in the field. The creation of the reference library of footprint images from captive tapirs was exceptionally time-consuming and incurred in quite a few related costs, including travelling expenses for several trips to the Sorocaba Zoo in São Paulo. Most importantly, the development of FIT for lowland tapirs required considerable amounts of time and financial resources on the part of WildTrack researchers who processed almost 1,000 tapir footprint images initially added to the reference library, developed and validated the algorithm, and later analysed hundreds of tapir footprint images collected in the field in Morro do Diabo. The entire process took almost three years. Regardless, these are one-off costs now that the algorithm for lowland tapirs has been established and is ready to be used by other lowland tapir researchers whenever appropriate. It is important to point out that FIT may not be a suitable methodology to be used inside dense forest. FIT is heavily dependent on the likelihood of finding long, clear sets of footprints, which may be unlikely inside the forest. In Morro do Diabo, I benefited from using internal dirt roads inside Morro do Diabo, where I had a perfect, sandy substrate to work with. There have been attempts to sample lowland tapir footprints for the use of FIT in the Peruvian Amazon, but the resulting sets of photos were not satisfactory for FIT analyses. The great majority of the footprints were photographed in deep mud substrate in the vicinities of salt licks or in the forest floor usually covered with leaves, therefore not providing a clear view of the contours of the footprints.

4.4.1.2 Comparing Density Estimators: Invasiveness of the Method

Another criterion I would like to add to the discussion of advantages and disadvantages of each methodology used is the level of invasiveness of the method. There is a growing trend in wildlife biology toward research methods that are less invasive. Over the past few years, the wildlife research community has been working on the development and application of several non-invasive field research techniques using sign survey methods for gaining information about animal populations. Some examples of animal signs that can be used include footprints, pictures taken by camera-traps, faecal and hair samples (Van Dyke *et al.* 1986; Koster & Hart 1988; Petrak 1990; Putman 1990; Smallwood & Fitzhugh 1993; Smallwood & Fitzhugh 1995; Zielinski & Stauffer 1996; Komers & Brotherton 1997; Noss *et al.* 2003). Indeed, non-invasive genetic methods have recently been developed and applied to estimate population sizes through DNA extracted from animal samples such as faeces and hair (Kohn *et al.* 1999; Banks *et al.* 2003; Eggert *et al.* 2003; Flagstad *et al.* 2004; Bellemain *et al.* 2005). Indirect methods have advantages in that they are relatively inexpensive, logistically straightforward and they do not require direct contact with the target animals (Putman 1984; Clevenger 1993).

While telemetry studies provide researchers with unparalleled data on ranging behaviour and habitat use among others, it is an extremely invasive method as it requires the capture and immobilisation of the animals for the placement of radio-collars. In most cases, animals must be recaptured several times for replacement or removal or collars. This is an important issue as there is a rapidly growing body of empirical evidence outlining the behavioural and physiological effects of repeat immobilisation and concomitant capture stress (Alibhai *et al.* 2001a; Alibhai *et al.* 2001b). Line-transect sampling does not require direct manipulation of the animals, but it can still affect animal behaviour through the encounters during data collection. The Footprint Identification Technique, on the other hand, is completely non-invasive as it does not require any type of contact between the researcher and the study animal. FIT was developed under the principle that the future of wildlife conservation depends to a large extent on the development of non-invasive methods of censusing and monitoring wildlife populations. For species which inhabit a landscape in which individuals regularly produce clear footprints and whose foot is of sufficient complexity to create a footprint with individual characteristics, tracks may serve as an alternative for natural marks. When compared with more direct methods, such as mark-recapture or radio-tracking, the data gained from sign surveys may not be as rigorous (Servin *et al.* 1987). However, while it is very difficult and time-consuming to capture a large enough number of animals for a telemetry study, using non-invasive methods researchers can sample larger number of animals.

An indirect, non-invasive method that has been commonly used to study lowland tapirs is camera-trapping (Noss *et al.* 2003; Trolle *et al.* 2007). Noss *et al.* (2003) used camera-traps simultaneously with telemetry to estimate lowland tapir ranging behaviour and population density in Kaa-Iya del Gran Chaco National Park, Bolivia, and compared both methods. The authors noted that while radio-telemetry provided considerably more precise and complete information on ranging patterns, camera-trapping provided more precise density estimates. However, while camera traps are acknowledged as important tools for monitoring cryptic species and estimating population size of naturally marked animals by means of well consolidated capture-recapture models (Karanth 1995; Karanth & Nichols 1998), their ability to individually identify non-spotted or non-striped animal species such as lowland tapirs is debatable (Oliveira-Santos *et al.* 2009).

4.4.1.3 Comparing Density Estimators: Accuracy of Estimates

Ten different estimates of tapir population density for Morro do Diabo were obtained: 6 estimates were obtained through 4 different analytical methods using radio-telemetry data; 1 was obtained by nocturnal line-transect sampling; and, 3 were obtained through 3 analytical methods using data from Footprint Identification Technique (FIT). The resulting tapir densities varied from a low estimate of 0.21 tapirs km^{-2} to a high estimate of 1.35 tapirs km^{-2}. Thus, it was deemed necessary to examine this variation in density estimates as well as the accuracy of each method before using any of these estimates to calculate tapir population sizes.

Karanth (1995) has argued that the presence of untagged animals in the population limits the usefulness of the radio-telemetry approach for estimating population density. In other words, the fact that it may not be possible to radio-collar all resident individuals in a given area can lead to an underestimation of population density, which will in turn affect the estimate of population size. Nevertheless, the main strength of most telemetry density estimates relies on the fact that they are strongly based on animal ranging behaviour parameters. This is deemed to be correct in long-term studies during which a large number of individuals is monitored therefore providing precise results of home range size and home range overlap, which is the case of this study in Morro do Diabo.

The tapir population density obtained by radio-telemetry Method 2 (0.34 tapirs km^{-2}) was considered to be the most appropriate estimate within the study, and all the other estimates were compared against it. This density estimate took into consideration the mean home range size of 4.7 km^2 and mean home range overlap of 37% calculated for the 14 tapirs radio-tracked from 8-36 months. At any rate, two other radio-telemetry density estimates provided very similar results. Radio-Telemetry Method 3, based on the number of radio-tracked tapirs divided by the Effective Sampled Area (KDE95%) and extrapolation of the obtained value to the entire area of 370 km^2 of Morro do Diabo, resulted in an estimate of 0.33 tapirs km^{-2}. Radio-telemetry Method 4, based on the calculation of mean values of home range radius and placement of circular buffers around locations of tapir captures to calculate Effective Sampled Area, resulted in an estimate of 0.32 tapirs km^{-2}. These three density estimates incorporated home range overlap in some manner, while radio-telemetry Method 1, based on the extrapolation of mean tapir home range size to the entire area of 370 km^2 of Morro do Diabo, did not. Therefore, Method 1 resulted in considerably lower density estimates of 0.21 tapirs km^{-2} (KDE95%) and 0.23 tapirs km^{-2} (MCP95%).

Results provided in Chapter 3 demonstrated that tapirs in Morro do Diabo exhibited extensive home range overlap between neighbouring individuals, usually around 30%, but sometimes as high as 90%. Extensive overlap was observed between pairs of the same and different sexes, as well as between pairs of same and different age classes. In addition, several examples of strong overlap of core areas of use were observed. Other studies on tapirs have also identified high percentages of home range overlap. Noss *et al.* (2003) obtained a mean home range overlap of 43.5% for lowland tapirs in Kaa-Iya del Gran Chaco National Park, Bolivia. In the same site in Bolivia, Ayala (2003) found home range overlaps of 80% between an adult male and a juvenile male, and a 30% overlap between the same juvenile male and an adult female. Foerster & Vaughan (2002) observed a mean home range overlap of 33.2% for Baird's tapirs in Corcovado National Park, Costa Rica. Thus, it appears to be critical that a density estimator for tapir species incorporates home range overlap in order not to underestimate population size.

The great majority of lowland tapir density estimates available in the literature have been obtained by diurnal line-transect sampling (Bodmer *et al.* 1994; Cullen *et al.* 2000; Peres 2000; Zimmerman *et al.* 2001; Cordeiro 2004; Desbiez 2010). However, most studies on lowland tapir activity patterns have demonstrated that this species is primarily nocturnal and crepuscular (Ayala 2002; Maffei *et al.* 2002; Wallace *et al.* 2002; Ayala 2003; Noss *et al.* 2003; Trolle 2003; Goméz *et al.* 2005; Tobler 2008). Indeed, the results on tapir activity patterns obtained through this telemetry study in Morro do Diabo have confirmed this pattern (Chapter 5). Therefore, a critical methodological question presents itself. Would not nocturnal line-transect sampling be a more suitable technique for assessing lowland tapir population density and surveying tapir populations? Answering this question would not be beneficial only to lowland tapirs, but to all four tapir species.

Cullen *et al.* (2000) carried out a diurnal line-transect mammal survey in Morro do Diabo, and obtained an estimate of lowland tapir density for the area. In 2006, I started a nocturnal line-transect sampling for the species in Morro do Diabo, to attempt to answer the question above. Thus, I selected the same line-transects used by Cullen *et al.* (2000) (internal dirt roads distributed throughout the area of Morro do Diabo) so that our results could be compared.

While Cullen *et al.* (2000) censused his transects from 06:00-10:00 h, and again from 15:00-19:00 h, with a much greater sampling effort for diurnal species, I concentrated the sampling effort on the main period of tapir activity in Morro do Diabo. Telemetry results from Morro do Diabo had already shown that the main period of activity of monitored tapirs was from 19:00-24:00 h, with a strong peak between 20:00-21:00 h (63% active). Therefore, I designed the nocturnal line-transect census to be carried out from 18:00-23:00 h, focusing data collection 2 hours before, during, and 2 hours after the main peak of tapir activity. In fact, the nocturnal line-transect sampling itself obtained the highest percentage of tapir encounters (47%) from 20:00-21:00 h, corroborating the results obtained by telemetry.

The results obtained by nocturnal line-transect sampling were largely different when compared to results obtained by Cullen *et al.* (2000). Cullen *et al.* (2000) had 8 tapir sightings with a sampling effort of 18 months of data collection, and obtained a tapir density estimate of 0.41 tapirs km^{-2} (95%CI, 0.20-0.84 tapirs km^{-2}). During the nocturnal census, I had 81 tapir encounters (actual tapir sightings or tapirs that were heard) in 20 months of data collection and 1,140 km walked, and obtained a tapir density of 1.35 tapirs km^{-2} (95%CI, 0.64-2.86 tapirs km^{-2}). It was thus evident that concentrating line-transect sampling during peaks of tapir activity increased the number of tapir sightings and consequently the density estimate. The reliability of line-transects to estimate density depends largely on the sample size of observations (Burnham *et al.* 1980; Buckland *et al.* 1993; Wilson *et al.* 1996). However, while the higher number of sightings obtained by nocturnal line-transect sampling provided some indication that this could be a more suitable method to survey tapirs, the resulting density estimate appeared to be exceedingly high for the species, particularly in the semi-deciduous forests of Morro do Diabo. This becomes particularly evident when comparing this estimate with the tapir density previously selected as the most appropriate within the study in Morro do Diabo (0.34 tapirs km^{-2}, radio-telemetry Method 2). I identified two very high estimates of lowland tapir density in the available literature: 2.20-2.50 tapirs km^{-2} in the Atlantic Forest of the Interior of Paraná State, Brazil (Rocha 2001), and 3.3-3.7 tapirs km^{-2} in the dry Amazon forests of Maracá Ecological Station in Roraima State, Brazil (Mendes-Pontes 2004). However, these studies applied non-replicable or questionable methods, and are therefore not comparable to the results of this study.

The overly high density estimate obtained by nocturnal line-transect sampling might be related to three different factors. First, I obtained a high frequency of encounters with tapirs walking on the roads (transects). Harmsen *et al.* (2009) used camera-trap and track data to analyse the detection probabilities of several Neotropical mammals on trails in dense secondary forests in Belize. While the camera-trap capture rates of Baird's tapirs were high in off-trail locations, Baird's tapir tracks were only found following trails. Harmsen *et al.* (2009) observed that half of the tapir footprint sets re-entered the forest within 1 km, indicating that they left larger trails and created their own paths through the forest. During this study in Morro do Diabo, I observed the same pattern. Long sets of tapir footprints were constantly observed along the internal roads of Morro do Diabo, many of them used as line-transects for nocturnal line-transect sampling. Tapirs regularly used these roads to travel in between different parts of their home ranges and this violates the DISTANCE sampling assumption that animals are randomly distributed. However, I still had to use these roads as line-transects so that the results of this study could be compared to Cullen *et al.* (2000). The second factor relies on the fact that one of the line-transects (Figure 4.1, line-transect 8, Aeroporto) was located along the south eastern border of Morro do Diabo, and one of its sides (opposite to the forest edge) was a crop field. As a consequence, on the crop field side of this particular transect, I had a visibility of over 100 m and a number of tapirs were sighted within that range. Both of these problems were identified in the very beginning of DISTANCE analysis. In an attempt to solve them, I established left data truncation at distance 0.1 m and right truncation at 35 m (estimated maximum visibility in the forested environment of Morro do Diabo), and the DISTANCE's Data Filter discarded all outliners from the dataset. This procedure should have solved these problems.

The third factor which may have also contributed to the high density estimate obtained by nocturnal line-transect was, once more, related to the transect that bordered the crop field. For the most part of the 20 months of nocturnal census, this field was planted with corn and tapirs appeared to be attracted to it. As a consequence, this was the line-transect where I had the highest percentage of tapir encounters (39%), also probably due to the fact that I was censusing during peaks of tapir activity. The other seven transects presented nearly even percentages of encounters. Given that DISTANCE assumes a random distribution of animals throughout the study area, the high percentage of tapir encounters in this particular transect most certainly affected the final density estimate. Thus, this transect should probably have been removed from the analysis. One might argue that another factor that could have led to this high density estimate could be double counting of individual tapirs along the line-transect. However, I have no evidence that this has happened.

This was the very first study to attempt the application of WildTrack's Footprint Identification Technique (FIT) for the estimate of tapir population density. The only previous study to apply a similar approach was carried out on mountain tapirs in Los Nevados National Park, Colombia, using a multivariate analysis of eight variables measured in left rear mountain tapir footprints to estimate population density (Lizcano & Cavelier 2000a).

The analyses of 27 sets of tapir footprint images photographed in a section of Morro do Diabo successfully identified 13 different individuals in the sample, including 10 females and 3 males. The lowland tapir foot proved to be of sufficient complexity to create footprints with specific characteristics appropriate for individual identification. The accuracy of correct classification of the FIT algorithm for lowland tapirs was over 90%.

Among the density estimates obtained by FIT, the one where Effective Sampled Area (ESA) was based on the home range radius provided by the mean distance between photos of footprints of the 13 identified tapirs (Method 1), resulting in an estimate of 0.43 tapirs km^{-2}, was the only estimate completely based on the FIT's dataset of footprints. The other two FIT density estimates were based on either home range (Method 2) or capture-recapture (Method 3) data to calculate home range radius. Thus, Method 1 was the only one to provide a density estimate that could allow for a full assessment of the reliability of this technique on estimating tapir density without the support of other data.

The home range radius calculated by FIT Method 1 was 1,091 m, which was much lower than the home range radius obtained from the home range size of the seven tapirs radio-tracked in the centre of Morro do Diabo (1,672 m, FIT Method 2) or from data on tapir capture-recapture in different traps (1,270 m, FIT Method 3). Therefore, the FIT estimate through Method 1 resulted in a smaller ESA and a higher density estimate, when compared to Methods 2 and 3.

When compared to the selected density estimate obtained by radio-telemetry Method 2 (0.34 tapirs km^{-2}), the FIT estimate of 0.43 tapirs km^{-2} appears to overestimate tapir density in Morro do Diabo. This may be attributed to three different factors. First, the area sampled for FIT (two internal dirt roads in the centre of Morro do Diabo) may not have been large or inclusive enough to cover the entire home ranges of the 13 identified tapirs. This may have led to an underestimate of home range radius, thus resulting in a smaller ESA and a higher estimate of density. This provides evidence that it would have been advisable to sample a larger area. The fact that data collection was concentrated on the roads might have been a limiting factor as well, given that tapirs might have used these roads intensively. Second, the FIT sampling in Morro do Diabo was carried out for only three months and it is quite possible that I have not managed to photograph the footprints of all resident tapirs in the area. The cumulative curve of number of different individual tapirs identified over time did not reach an asymptote. Therefore, it is probable that had I continued sampling the area for a longer period of time, additional tapirs would have been identified, thus changing the final density estimate. Third, the 1,091 m FIT estimate of home range radius was considerably lower than the mean home range radius obtained by radio-telemetry (1,616 m, Chapter 3, Table 3.5), which is by itself evidence that the FIT home range radius was underestimated.

Noss *et al.* (2003) noted that the buffer width estimated from mean maximum distance covered by individual lowland tapirs during camera trap surveys (1.2-1.3 km) was very similar to the average of half the distance across home ranges of five radio-tracked individuals (1.35 km), which confirmed that the ESA was measured appropriately. On the other hand, Soisalo & Cavalcanti (2006) used both camera-traps and radio-telemetry to study jaguars in the Brazilian Pantanal and noted that the jaguar home range radius calculated by radio-telemetry was twice the length of the radius calculated by photo captures. Therefore, Soisalo & Cavalcanti (2006) suggested that the home range radius calculated from camera-traps can be underestimated and consequently overestimate jaguar density.

FIT was designed by WildTrack researchers to survey "closed" animal populations with the final result being total animal counts. The use of FIT to sample a small, "open" section of

Morro do Diabo and then extrapolate the estimated tapir density in an ESA to the entire area of 370 km^2 of Morro do Diabo proved to be quite a challenge. The main difficulty was the determination of ESA. At any rate, if the projected figure of 13 lowland tapirs for the sampled section of Morro do Diabo is deemed to be correct, then this indicates that FIT could be a practical and reliable method for censusing and monitoring lowland tapir populations in habitats where individuals regularly produce clear footprints. Moreover, since this method is based on track versus track comparisons, it would be a reliable method for monitoring individual movement patterns as well. For example, during this study, which was carried out over a relatively short period of time, for Tapir #7 there appeared to be 8 different localities where its footprints were photographed, thus providing information about the movement patterns of this tapir. Furthermore, since there appeared to be a marked consistency in the relatedness of tracks and gender/age class predictions, it is safe to conclude that the gender/age class predictions are likely to be accurate. This study also demonstrated that it was possible to successfully develop the FIT algorithms for lowland tapirs using footprint images from captive individuals.

4.4.2 Lowland Tapir Population Density in Morro do Diabo State Park

The estimates of lowland tapir density reported in the literature are quite variable (Chapter 2, Table 2.7). Lowland tapir population density ranges from a high estimate of 1.6 tapirs km^{-2} in undisturbed, non-hunted, or lightly hunted Neotropical forest sites (Robinson & Redford 1986; Robinson & Redford 1991) to less than 0.3 tapirs km^{-2} in different parts of the species distribution range (Cullen *et al.* 2000; Aquino *et al.* 2001; Aquino & Calle 2003; Desbiez 2010). This variation in density estimates can be explained by several different factors including differences in environments, habitat types studied, levels of habitat conservation, different levels of hunting and, most importantly, differences in the methods used. Evidence of variation in density estimates due to methods applied is well illustrated in this lowland tapir study. The 10 different tapir density estimates obtained by three different density estimators and several analytical methods varied from 0.21-1.35 tapirs km^{-2}.

Nevertheless, the density estimate based on radio-telemetry results of tapir home range size and home range overlap was selected as the most appropriate for Morro do Diabo (0.34 tapirs km^{-2}). When comparing this estimate with other lowland tapir densities obtained by radio-telemetry in other parts of the species distribution range, the tapir density in Morro do Diabo appears to be lower. Ayala (2003) conducted a telemetry study on lowland tapirs in Kaa-Iya del Gran Chaco National Park, Bolivia, and obtained a density of 0.50 tapirs km^{-2}. In the same national park in Bolivia, Noss *et al.* (2003) estimated the lowland tapir density to be 0.71 tapirs km^{-2}. Noss *et al.* (2003) noted that tapirs in the dry Chaco forests have successfully adapted to conditions of seasonal drought and appeared to sustain relatively high population densities, provided that they were protected from hunting.

I attribute the lower tapir density in Morro do Diabo to three main factors. First, the difference seems to be largely associated with larger home range sizes. The mean home range size calculated for the 14 tapirs radio-tracked from 8-36 months in Morro do Diabo was 4.7 km^2 when estimated by KDE95%, and 4.4 km^2 when estimated by MCP95% (Chapter 3), both of which larger than most radio-telemetry estimates obtained for the species in other areas. Noss *et al.* (2003) obtained a mean home range size of 2.5 km^2 (MCP95%) in Kaa-Iya del Gran Chaco National Park, Bolivia. Tobler (2008) carried out a GPS telemetry study on lowland tapirs at Los Amigos Conservation Concession in the Peruvian Amazon and obtained a mean home range size of 2.6 km^2 by KDE95%, and 2.2 km^2 by MCP95%. The larger home range sizes in Morro do Diabo can be attributed to the lower carrying capacity of the heterogeneous, semi-deciduous Atlantic Forests. The primary production of semi-deciduous forests is lower and more erratic when compared to moister forests and, at the same time, water availability is lower (Cullen *et al.* 2001a). Therefore, tapirs in semi-deciduous forests most probably need their home ranges to be large enough to include large expanses of forest in order to incorporate all the different habitat types they need and prefer (Chapter 5), ultimately fulfilling their nutritional and water requirements.

Second, the lower tapir density in Morro do Diabo might be associated with the extensive fragmentation of the Atlantic Forest of the Interior. Population density is limited to the number of animals that a given area can support (Robinson & Redford 1986). Forest reduction and fragmentation are generally accompanied by a loss of habitat diversity, which in turn affects resource diversity (Wright & Duber 2001; Tabarelli *et al.* 2004). While both Kaa-Iya del Gran Chaco National Park (34,400 km^2) in Bolivia, as well as Los Amigos (1,400 km^2) in Peru, consist of much larger expanses of contiguous habitat, Morro do Diabo is a relatively small forest fragment of 370 km^2 immersed in a landscape matrix of agricultural and pastoral land. Although recent, the processes of destruction and fragmentation of the Atlantic Forests of the Pontal do Paranapanema Region have most certainly led to a reduction in habitat diversity and consequently in carrying capacity of Morro do Diabo. It is also important to mention that before its establishment as a protected area in 1986, the forests of Morro do Diabo had already suffered from a number of additional processes of habitat degradation. These included the construction of both a railway and a highway crossing Morro do Diabo in different places, the clearing of several patches of forest within Morro do Diabo for the extraction of timber, the selective logging of valuable hard woods, and several major fire events (Faria & Pires 2006). All these events have contributed to the loss of habitat diversity in Morro do Diabo.

The third factor that could have potentially contributed to the lower tapir density in Morro do Diabo is the presence of healthy populations of jaguars and pumas. Cullen (2007) estimated a jaguar population of 13 individuals (95%CI 11-22) in Morro do Diabo and observed that tapirs were an important prey item for these cats. Data and anecdotal information collected during this study in Morro do Diabo included several records of tapir predation by large cats. Three out of 25 radio-collared tapirs were predated by large cats. An adult female and a sub-adult male tapirs were predated by jaguar, and one sub-adult male tapir was predated by puma. Three carcasses of non-tagged adult tapirs killed by jaguars were found in different areas of Morro do Diabo during the study. Several of the captured tapirs presented scars, apparently from large cat attacks. Park rangers reported two sightings of jaguars chasing tapirs along the shoreline of the Paranapanema River. Therefore, while jaguars and pumas naturally prefer small- to medium-sized preys (Polisar *et al.* 2003; Astete *et al.* 2008), in Morro do Diabo these cats appear to prey on tapirs regularly. As a consequence, it seems pertinent to consider tapir predation by large cats as one of the components of tapir population regulation in Morro do Diabo. Fragmented landscapes are known to exacerbate the effect of predation on prey population dynamics in different ways, one of them by allowing carnivores to concentrate their hunting efforts on islands of preferred prey habitat (Wirsing *et al.* 2002).

When looking at radio-telemetry density estimates obtained for other tapir species, results once more vary. Nevertheless, overall, lowland tapirs appear to occur at higher population densities than the other three species. Williams (1984) radio-tracked Baird's tapirs in the dry forests of Santa Rosa National Park, Costa Rica, and estimated a density of 0.21 tapirs km^{-2}. Foerster (1998) carried out a long-term telemetry study on Baird's tapirs in Corcovado National Park, Costa Rica, and obtained a much higher density (1.6 tapirs km^{-2}). Corcovado National Park is a unique area with an extremely high diversity and availability of resources, particularly fruit, which certainly allows for a much higher carrying capacity and higher density of tapirs (Foerster & Vaughan 2002). Mountain tapir telemetry density estimates appear to be much lower when compared to lowland and Baird's tapirs. Downer (1996) estimated a mountain tapir density of 0.17 tapirs km^{-2} in Sangay National Park, Ecuador. Lizcano (2006) used GPS telemetry to study mountain tapirs in Los Nevados National Park, Colombia, and estimated a density of 0.10 tapirs km^{-2}. The only density estimate I found for Malayan tapirs used a combination of tapir signs on line-transects and camera-traps, resulting in an estimate of 0.15 tapirs km^{-2} in Kerinci Seblat National Park, Sumatra (Andri 2006).

4.4.3 Lowland Tapir Population Sizes in the Atlantic Forests of the Pontal do Paranapanema Region and Implications for Population Viability

Population size is a critical demographic attribute and the single most important parameter to determine species extinction risk (Shaffer 1981; Gilpin & Soulé 1986; Lacy 1993; Lacy 2000;

Shaffer *et al.* 2000; Aurambout *et al.* 2005). Whereas controversy remains as to how large populations need to be to ensure the viability of a given species over the long-term (Lande 1995; Lynch & Lande 1998; Reed & Hobbs 2004), population size is considered to be the major determinant of species long-term persistence in a given area (Diamond *et al.* 1987; Newmark 1987; Pimm *et al.* 1988; Richman *et al.* 1988; Soulé *et al.* 1988; Berger 1990; Schoener & Spiller 1992; Foufopoulos & Ives 1999). The tapir density estimates obtained in Morro do Diabo varied. Consequently, the estimates of tapir population size ranged from 79 (radio-telemetry, Method 1) to 499 (nocturnal line-transect sampling) tapirs in Morro do Diabo. Nevertheless, the selected telemetry density estimate of 0.34 tapirs km^{-2} was used to derive tapir population sizes in Morro do Diabo and seven Atlantic Forest fragments where the presence of tapirs had been previously confirmed (Ditt 2002).

The population size estimates resulted in ~130 tapirs in the 370 km^2 of forests of Morro do Diabo, and no more than 22 additional individuals distributed in the seven forest fragments. Three of the forest fragments were larger than 10 km^2 and resulted in tapir populations from 4-6 individuals each. Four of the forest fragments were much smaller (4-5 km^2), and did not appear to hold up more than 2 tapirs each. In total, the Atlantic Forests of the Pontal do Paranapanema Region should include ~150 tapirs in 8 main patches of forest.

While Morro do Diabo hosts a rather large tapir population, the smaller forest fragments fail to provide enough space for more than just a few individuals each. Wide-ranging species with large spatial requirements - such as tapirs - generally cannot survive in small areas over the long-term (Redford & Robinson 1991). Chiarello (1999) analysed the effects of the Atlantic Forest fragmentation on mammal communities, and observed that tapirs were present in large patches but not recorded in small forests. Such reduced tapir populations in the small forest fragments of the Pontal do Paranapanema Region are most certainly not large enough to persist over the long-term. In fact, even if we considered some of the higher density estimates obtained during this study in Morro do Diabo, the resulting population sizes in the small fragments would still be too small to ensure long-term persistence.

This scenario could potentially be even worse if we considered that tapirs in the smaller Atlantic Forest fragments in the Pontal do Paranapanema Region may not occur at the same density as observed in Morro do Diabo. Morro do Diabo is a relatively large patch of protected forest, which overall benefits from a higher level of habitat conservation. Therefore, it certainly has a higher carrying capacity for tapirs and other species. It is quite possible that tapirs in the forest fragments might have even larger spatial requirements in order to fulfil their resource needs. In that case, the tapir population numbers in the small forest fragments would be even lower. During this study, I have not obtained specific tapir densities for the small forest fragments in the Pontal do Paranapanema Region. As a result, by using the tapir density obtained in Morro do Diabo to estimate tapir numbers in the forest fragments, I may have overestimated tapir population sizes in these small forests. Evidence that tapirs might occur at a higher density in Morro do Diabo when compared to the small forest fragments of the Pontal do Paranapanema Region was provided by Cullen *et al.* (2000). While the authors estimated the tapir density in Morro do Diabo to be 0.41 tapirs km^{-2}, a lower density of 0.30 tapirs km^{-2} was estimated for a smaller patch of forest (2.1 km^2).

Other factors, in addition to fragment size, must be considered when estimating tapir population sizes and assessing tapir viability over the long-term. One of these factors is the loss of habitat diversity caused by forest fragmentation, which in turn affects the diversity and availability of resources (Wright & Duber 2001; Tabarelli *et al.* 2004). There is growing evidence that, when compared to contiguous tracts of forest, the availability of fruit resources in small forest fragments is lower (Terborgh 1986; Terborgh 1992). This is a major limiting factor for the persistence of frugivore species such as tapirs. Tófoli (2006) analysed the impact of fragmentation of the Atlantic Forests of the Pontal do Paranapanema Region on the diet of tapirs and showed that tapirs in Morro do Diabo consumed significantly higher percentages of fruit and lower percentages of fibrous material when compared with tapirs in the smaller forest fragments. In addition, estimates of fruit species richness in the diet of tapirs indicated considerably higher fruit diversity in Morro do Diabo than in the forest fragments (Tófoli 2006). In general, fragmented habitats fail to provide the necessary resources to support species assemblages found in intact habitats. This leads to a general reduction in the number of individuals that can be hosted (Lovejoy *et al.* 1984; Quinn & Hastings 1987; Bierregaard *et al.* 1992; Burkey 1993; Kattan & Alvarez-Lopez 1996). When it comes to frugivore species, a suite of resource-related factors such as spatial distribution of fruit sources, total fruit availability, seasonal fruit availability, and severity of fruit scarcity periods, will affect habitat use and spatial requirements in fragmented habitats (Wright *et al.* 1999; Fleury & Galetti 2004; Keuroghlian & Eaton 2008), which will ultimately affect population size.

The conservation status, levels of habitat disturbance, and impact of existing threats in these small areas of forest must also be considered when evaluating population size. Besides Morro do Diabo, the only other protected area in the Pontal do Paranapanema Region is the Black-Lion-Tamarin Ecological Station, created in 2002. This protected area encompasses the four largest forest fragments in the region: Santa Maria Cachoeirinha (18.3 km^2), Tucano (18 km^2), Ponte Branca (13 km^2), and Água Sumida Estrela da Alcídia (12.1 km^2) (Chapter 2, Figure 2.6). Tapirs are known to be present in three of these forest fragments, the only exception being the Tucano fragment (Ditt 2002). All the other forest fragments in the Pontal do Paranapanema Region lie within private properties or Agrarian Reform settlements (owned by the State), therefore lacking legal protection. Some of these forests were left standing in obedience to the Brazilian law that obligates landowners within the Atlantic Forest domain to maintain 20% of their land covered with original forests (Cullen 1997). As a consequence of the lack of effective protection of these areas, the activities of rural communities living in the vicinities of Morro do Diabo and other forest fragments in the region have been leading to a gradual loss of biodiversity (Cullen 1997). Practices of illegal hunting, erosion of forest edges by fires and cattle grazing, as well as the spread of aggressive weeds, and pesticides have been seriously modifying forest structure and reducing habitat quality and carrying capacity for a number of species.

Although the above-mentioned law protects these forest fragments from further cutting or use, tapir populations in these fragments suffer from higher levels of illegal hunting when compared to Morro do Diabo. Hunting activities in the Pontal do Paranapanema Region are more of sport or recreational rather than subsistence or commercial activities, mostly because of the lack of traditional hunting practices, the small size of fragments, and the biomass of game (Cullen 1997). However, hunting in this region is still a cherished past-time for men and adds variation in the diet. While peccaries, deer, armadillos and agoutis are largely preferred by hunters in the region, tapirs are also sought after (Cullen 1997). The low rates of population growth, long generation time, and long reproductive cycles, are life-history characteristics that make tapirs particularly susceptible to overhunting, which considerably increases the likelihood of extirpation of small tapir populations (Bodmer *et al.* 1997). Cullen *et al.* (2000) compared the abundance of mammalian species in slightly and heavily hunted fragments of Atlantic Forest of the Interior - including Morro do Diabo as one of the slightly hunted sites - and observed that tapirs could not cope with persistent hunting and were extirpated from heavily hunted sites. In fact, tapirs were observed to be locally extinct in six out of 13 forest fragments surveyed in the Pontal do Paranapanema Region (Ditt 2002). This could be at least partially attributed to overhunting.

Tapirs are wide-ranging species and have the ability to traverse areas of low quality habitat in order to move through the landscape matrix in between patches of forest (Flesher 2007). During this study, I gathered a considerable amount of data and anecdotal information on tapir movements throughout the fragmented landscape of the Pontal do Paranapanema Region. Two of the radio-collared tapirs in the western border travelled regularly between Morro do Diabo and the 4.2 km^2 Ribeirão Bonito forest fragment (Chapter 3, Figure 3.5). In addition, tapir footprints, faeces and foraging signs were recorded in between the northern edge of Morro do Diabo and three forest fragments in that area. Also by using tapir signs, movement pathways were identified in between forest fragments located to the north, northwest, and northeast of Morro do Diabo. Lastly, park rangers provided a few reports of tapirs crossing the Paranapanema River in the southern limit of Morro do Diabo.

While the landscape crossings I am referring to were observed in rather short-scales (no further than 1.5-2.0 km) and at low rates, they provided evidence of the occurrence of a tapir metapopulation scenario in the Pontal do Paranapanema Region. The fact that tapirs in the Pontal do Paranapanema Region appear to move fairly easily through areas of non-natural habitat indicates that the landscape matrix of the region provides a certain level of functional connectivity for them (Greenberg 1989; Sieving *et al.* 1996). In other words, the inter-habitat matrix permeability in the Pontal do Paranapanema Region appears to be reasonable for tapirs. Functional connectivity depends on the landscape pattern, but most importantly on the interactions between this pattern and the biological characteristics of the target species, such as their ability to traverse areas of low quality habitat (Greenberg 1989; Sieving *et al.* 1996). Given that connectivity is a vital parameter for the persistence of animal species in severely fragmented landscapes (Karr 1982; Blake & Karr 1987; Bierregaard & Stouffer 1997; Stratford & Stouffer 1999; Crooks *et al.* 2000; Uezu *et al.* 2005), the functional connectivity observed for tapir populations in the Pontal do Paranapanema Region could potentially facilitate their persistence over the long-term.

The functional connectivity of the tapir population of the Pontal do Paranapanema Region will only be maintained if Morro do Diabo remains well protected. Preliminary results of a large scale lowland tapir survey currently underway throughout the entire range of the Atlantic Forest biome has already shown that tapirs rarely survive in forests smaller than 20 km^2 without recourse to larger forest patches (Flesher 2007). While tapirs appear to persist in some areas where habitat is reduced to small scattered fragments, they need recourse to fragments larger than 5 km^2 in clusters that total at least 15 km^2. In contrast, tapirs disappear completely in landscapes where all the forest fragments are smaller than 5 km^2, even when these fragments constitute a large percentage of the landscape (Flesher 2007). Novaro *et al.* (2000) noted that demographic characteristics of tapirs determine lower dispersal ability when compared to other Neotropical species. Thus, the persistence of tapirs at sites where potential sources of dispersers exist (Novaro *et al.* 2000) corroborates the prediction that even low levels of dispersal may be sufficient to maintain populations in sink areas (Pulliam 1988).

In conclusion, the long-term persistence of the lowland tapir populations in the Atlantic Forests of the Pontal do Paranapanema Region, particularly the smaller populations in the forest fragments, completely depends on the maintenance of the existing metapopulation dynamics. While the tapir populations in the small forest fragments are too small to be viable over the long-term, a viable metapopulation of 150 tapirs in the entire Pontal do Paranapanema Region may persist. In genetic terms, the short period since fragmentation occurred in the landscape of the Pontal do Paranapanema Region (5-6 tapir generations) probably means that patterns of genetic structure are still in transition, and therefore genetic drift and inbreeding have not been observed yet (Gonçalves da Silva 2007). Therefore, the maintenance of the tapir metapopulation dynamics can allow for genetic flow between different patches of forest, thus maintaining genetic diversity over the long-term. Nevertheless, in order to ensure the viability of this tapir metapopulation, several conservation measures must be implemented. First of all, Morro do Diabo must remain intact and effectively protected. Second, measures must be taken to ensure the permeability of the landscape matrix, therefore allowing for and facilitating tapir movements in between forest patches. Third, threats impacting tapirs in the smaller forest fragments, particularly hunting, must be neutralised. The tapir population in Morro do Diabo (130 tapirs) is not large enough to maintain a disrupted "source-sink" structure (Pulliam 1988; Hanski & Simberloff 1996), which could destabilise the metapopulation and seriously compromise persistence and viability over the long-term. If given proper conditions in terms of habitat quality and neutralisation of threats, tapirs might be capable of re-colonising the forest fragments from which they have been extirpated in the past.

Understanding the ecological interactions between animal populations and their habitat in fragmented landscapes is another important factor for the assessment of the viability of tapir populations over the long-term. The next chapter focuses on analysing the spatial and temporal interactions between tapirs and the different types of habitat found in the semi-deciduous forests of Morro do Diabo and its surrounding landscape. Results on tapir habitat use and habitat selection will be used to understand how tapirs establish and use their ranges in a forest fragment, thus offering hypotheses concerning their long-term persistence in the Pontal do Paranapanema Region.

Chapter 5

Spatial and Temporal Interactions between Tapirs and the Landscape

Photo by Patrícia Medici

5.1 Introduction

One of the main challenges in ecology is understanding the spatial and temporal distribution of animals in heterogeneous landscapes (Pusenius *et al.* 2000; Lin & Batzli 2001; Calsson-Granér & Thrall 2002), and how these patterns are determined by the interactions between these animals and the landscape (Lima & Zollner 1996; Turchin 1998; Wiegand *et al.* 1999; Matthiopoulos 2003). Studies on habitat requirements are usually used to address these questions. In-depth assessments of species' habitat requirements usually include a study of *habitat use*, *i.e.* "the extents to which different vegetative associations are used by an animal" (Hall *et al.* 1997), and then, based on these results, *habitat selection* (MacArthur & Pianka 1966; Neu *et al.* 1974; Rosenzweig 1981). The concept of habitat selection (MacArthur & Pianka 1966) is based on the evaluation of habitat *quality* or *suitability*, *i.e.* "the ability of the habitat to sustain life and support population growth" (Garshelis 2000). By selecting certain types of habitat, an animal attempts to maximise its survival, reproductive success, and the net rate of energy intake (Johnson 1980; Abrams 2000; Delibes *et al.* 2001). Presumably, species should survive and reproduce better (*i.e.* their fitness should be higher) in habitats that they tend to prefer (Rosenzweig & Abramsky 1986). Thus, once habitats can be ordered by their relative preference, they can be evaluated as to their relative importance in terms of fitness. By understanding the composition, availability, and selection of habitat patches required by a healthy, functioning population of tapirs, the landscape necessary for its long-term survival is explicitly defined.

According to classical theories of foraging and habitat selection, a forager should continue to exploit a patch until its harvest rate in the patch drops to its average over all patches (including foraging time in patches and travel time between patches) (Charnov 1976; Rosenzweig 1981). Under these conditions, the animal will spend most of its time in those habitats richest in food, and habitat selection is likely to reflect food availability. However, there are trade-offs between selecting different resources (Kotler 1997), such as between foraging and predator avoidance (Lima & Dill 1990; Turner 1997). Thus, it is likely that an animal's habitat selection may reflect a multitude of requirements that an individual must fulfil to successfully complete its life cycle, and not just availability of forage (Orians & Wittenberger 1991; Dunning *et al.* 1992; Mysterud *et al.* 2001). Furthermore, habitat selection is often a scale dependent process (Johnson 1980; Levin 1992), that is, different mechanisms and trade-offs that determine an animal's resource use may come into play on different spatial and temporal scales (Wiens 1989). Patch selection within the home range may depend on the activity patterns of an animal (Morris 1987; Morris 1992).

Understanding the ecological interactions between animal populations and their habitat in fragmented landscapes is an important factor for the assessment of the viability of these populations over the long-term. Losses of habitat quality and diversity in forest fragments are important proximal causes of species extinctions (MacArthur & Wilson 1967; Gilpin & Soulé 1986; Wilcove *et al.* 1986; Terborgh 1992). Hence, in addition to area restrictions and direct threats caused or facilitated by landscape fragmentation, factors related to habitat quality and diversity may also affect the persistence of animal populations in forest fragments. Some of these factors include topography, edaphic characteristics, and moisture gradients among others (Saunders *et al.* 1991; Wright & Duber 2001; Tabarelli *et al.* 2004; Keuroghlian & Eaton 2008). Most importantly, the process of habitat fragmentation leads to reductions in fruit diversity (Wright & Duber 2001; Tabarelli *et al.* 2004) and fruit availability (Terborgh 1986; Terborgh 1992), which is a particularly limiting factor for the long-term persistence of frugivore species such as lowland tapirs. Nevertheless, aspects of tapir habitat requirements in fragmented landscapes are largely unknown.

The lowland tapir has a broad geographic distribution (Hershkovitz 1954; Emmons & Feer 1990; Eisenberg 1997), and seems to be adapted to a wide range of habitat types (Medici *et al.* 2007a; Taber *et al.* 2008). In spite of that, a number of studies have identified patterns of habitat preference in tapir species (Bodmer 1990b; Fragoso 1991a; Fragoso 1991b; Naranjo 1995; Salas 1996; Foerster 1998; Naranjo & Cruz-Aldán 1998; Herrera *et al.* 1999; Muench 2001; Foerster & Vaughan 2002; Ayala 2003; Lizcano 2006; Tobler *et al.* 2006; Tobler 2008; Steinmetz *et al.* 2008). There is growing evidence that besides large home ranges, tapirs also require certain habitat types that contain the resources they need or prefer in order to survive and reproduce, and ultimately persist over the long-term.

The destruction and fragmentation of the Atlantic Forest of the Interior of the Pontal do Paranapanema Region is relatively recent when compared to areas in the eastern part of the biome. Despite the extensive loss of habitat, some of the larger forest fragments in the region, especially Morro do Diabo, still support tapir populations. Thus, the assessment of the ecological interactions between tapirs and their habitat in Morro do Diabo provided critical information on how tapirs use their ranges in a forest fragment, offering hypotheses concerning their long-term persistence in fragmented landscapes.

In this Chapter, I explore the aspects related to the spatial and temporal interactions between tapirs and the fragmented landscape of the Pontal do Paranapanema Region. This includes the interactions between tapirs and the different types of habitat available to them. I first looked at the extent of occurrence of different types of habitat within tapir home ranges and core areas of use in Morro do Diabo. This allowed me to gain some insight into how tapirs establish and structure their home ranges. Most importantly, this allowed me to examine what kinds of habitats tapirs incorporate within their home ranges and core areas of use, provided that aspects of intra-specific competition allow them to do so. Second, I focused on how tapirs actually use the different habitat types. I determined the availability and use of different habitat types within tapirs' home ranges, and examined which habitats were significantly selected or avoided by tapirs. The examination of habitat selection provided some perspective in terms of tapir habitat requirements, and whether tapir use of different habitat types occurred in proportion to their availability in the study site. Lastly, I analysed tapir activity patterns in Morro do Diabo, obtaining information about main peaks of activity, and examined patterns of habitat use in relation to activity. These analyses provided useful information about what types of habitat tapirs use for their main activities including foraging, travelling, and resting. All this information was then utilised to characterise the spatial and temporal interactions between tapirs and the mosaic of different habitats found within the landscape of the Pontal do Paranapanema Region, and how this relates to the survival and persistence of tapir populations in the Atlantic Forest over the long-term.

5.2 Methods

5.2.1 Radio-Telemetry

Radio-telemetry was used to study tapir ranging behaviour in Morro do Diabo. Ranging behaviour maps were then used to analyse habitat composition within tapir home ranges and core areas of use, as well as tapir habitat use and selection. The study of activity patterns was carried out through the use of radio-collars equipped with a mortality-motion sensor programmed with a 1-minute delay, which provided "active/alive" or "inactive/dead" pulse depending on the activity of the study animals. A complete overview of the use of radio-telemetry methodology and data analysis is provided in Chapter 3.

5.2.2 Habitat Composition within Tapir Home Ranges and Core Areas of Use

The analysis of habitat composition within tapir home ranges and core areas of use was carried out by superimposing tapir ranging maps onto Morro do Diabo's vegetation map (Faria & Pires 2006) in ArcGIS 9.X (ESRI-GIS Mapping Software, USA). This analysis was carried out separately for the different sections of Morro do Diabo where the study took place: (i) West Border (N=7 tapirs), (ii) Southeast Border (N=3), (iii) Centre (N=7), and (iv) Northwest Border (N=2), given that different habitat types were available to tapirs in each section. The analytical methods were the following:

1) Maps of home range (KDE95%) and core areas of use (KDE50% and KDE25%) of all 19 tapirs radio-tracked during the study were superimposed onto Morro do Diabo's vegetation map. Percentages of occurrence of each habitat type within the home range and core areas of use were calculated for each individual tapir. Results were then used to calculate mean percentages of occurrence of each habitat type within tapir home range and core areas of use in each section of Morro do Diabo.

2) Maps of home range used in dry and wet season (KDE95%) of the 14 tapirs radio-tracked from 8-36 months were superimposed onto Morro do Diabo's vegetation map. Percentages of occurrence of each habitat type within home ranges used in dry and wet seasons were calculated for each individual tapir. Results were then used to calculate mean percentages of occurrence of each habitat type within tapir home ranges used in dry and wet seasons in each section of Morro do Diabo.

5.2.3 Tapir Habitat Selection

5.2.3.1 Habitat Availability

The analysis of habitat availability was based on Morro do Diabo's vegetation map (Faria & Pires 2006) using ArcGIS 9.X (ESRI-GIS Mapping Software, USA). This analysis was carried out separately for the different sections of Morro do Diabo where the study took place, given that different habitat types were available to tapirs in each section. The first step of the analysis was to define the area available to radio-tracked tapirs in each section, which was done as following:

1) The total area used by radio-tracked tapirs in each section of Morro do Diabo was mapped as the total area making up their home ranges calculated using Kernel Density Estimator (KDE95%).

2) The area available to radio-tracked tapirs in each section of Morro do Diabo was extended by establishing a buffer around the total area which they used. The width of the buffer was calculated as half the Mean Maximum Distance Moved (½MMDM, home range radius) by tapirs radio-tracked in each section, as detailed in Chapter 3. The area encompassed by the limits of the buffer was then considered to be available to tapirs in each section of Morro do Diabo.

3) The maps of areas available to tapirs in each section were then superimposed onto Morro do Diabo's vegetation map. The availability of different habitat types within the delimited area available to tapirs in each section was calculated as a percentage.

5.2.3.2 Habitat Use

Using ArcGIS 9.X (ESRI-GIS Mapping Software, USA), I superimposed the maps of habitat availability in each section of Morro do Diabo with the locations of tapirs radio-tracked in each section. I obtained counts of tapir locations within each habitat type and calculated percentages of use of different habitat types separately for each section. The same procedures were performed for radio-tracking locations obtained in wet and dry seasons.

5.2.3.3 Habitat Selection Index

Percentages of availability of different habitat types and percentages of use of each habitat type were then used to analyse habitat selection. I used Manly's standardised habitat selection index for constant resources (Manly *et al.* 2002). Manly's standardised habitat selection index is based on the selection ratio W_i, which is the proportional use divided by the proportional availability of each habitat type: $W_i = o_i / n_i$

Where:

o_i = Proportion of the sample of used resource units in category i or proportion of habitat used

n_i = Proportion of available resource units in category i or proportion of habitat available

A W_i value larger than 1 indicates a positive selection for the habitat type and a value less than 1 indicates avoidance of the habitat. A value around 1 indicates that the habitat type was used proportionally to its availability and no habitat selection was noted. The preference/avoidance for each habitat was calculated from the selection ratio W_i and tested using a chi-square test adjusted by Bonferroni. These analyses were carried out with the ADEHABITAT extension of the statistical package R Version 2.9.0 (The R Project for Statistical Computing, R Development Core Team 2008).

5.2.4 Tapir Activity Patterns

Triangulation bearings of radio-collared tapirs were taken from two different fixed stations, and the activity of the animal at the moment (active, inactive) was recorded for each bearing. For this analysis, I used only the activity record obtained for the first bearing. As described in Chapter 3, the datasets of each radio-tracked tapir were screened and cleaned up for tapir ranging behaviour analysis. However, for the analyses of tapir activity patterns, I included all 7,537 locations before screening.

For all 19 tapirs radio-tracked in Morro do Diabo combined, I calculated percentages of activity and inactivity for each period of 1 hour. I then used these percentages to build a graph of activity patterns over a period of 24 hours. Additionally, I did the same analysis separately for both sexes and different age classes, as well as for all tapirs in wet and dry seasons. Main periods of tapir activity were considered to be those periods when tapirs were found to be active in over 50% of the locations. Main periods of inactivity were those periods when tapirs were found to be active in less than 30% of the locations. Peaks of activity were identified within main periods of activity.

5.2.5 Patterns of Tapir Habitat Use in Relation of Activity

I calculated percentages of active and inactive tapir locations obtained in different habitat types in the four different sections of Morro do Diabo where the study took place, and determined the types of habitat tapirs use for their main activities including travelling, foraging, and resting. These analyses were carried out for all tapir locations within their home ranges, as well as separately for wet and dry seasons.

5.3 Results

Ten different vegetation types are found in Morro do Diabo: (i) Tall mature forest; (ii) Low mature forest; (iii) Secondary forest in early stages of regeneration; (iv) Secondary forest in later stages of regeneration; (v) Cerrado (Savannah); (vi) Riparian forest along the Ribeirão Bonito stream; (vii) Riparian forest along the Paranapanema River; (viii) Low, dense forest in various stages of regeneration; (ix) Temporary lakes; and (x) Agricultural and pastoral land (outside the boundaries of Morro do Diabo) (Faria & Pires 2006).

5.3.1 Habitat Composition in Tapir Home Ranges and Core Areas of Use

Seven habitat types were found within the home ranges and core areas of use of tapirs radio-tracked in the western border of Morro do Diabo (Table 5.1). The most represented habitat type in tapir home ranges in the western border was Tall mature forest (33%), followed by Agricultural and pastoral land (16%). Likewise, Tall mature forest was the most strongly represented habitat type in the tapirs' core areas of use at the 50% level (30%), closely followed by Riparian forest along the Ribeirão Bonito stream (29%). The most strongly represented habitat type in the 25% core areas of use was Riparian forest along the Ribeirão Bonito stream (45%). Agricultural and pastoral land and Secondary forest in late stages of regeneration were the least represented habitat types in the core areas of use of tapirs in the west border. Tall mature forest was the most represented habitat type within tapir home ranges in both dry and wet seasons (Table 5.2).

Seven habitat types were found within the home ranges and core areas of use of tapirs radio-tracked in the south eastern border of Morro do Diabo (Table 5.1). The most represented habitat type in tapir home ranges in the south eastern border was Riparian forest along the Paranapanema River (31%), closely followed by Tall mature forest (30%). Likewise, Riparian forest along the Paranapanema River was the most strongly represented habitat type in the tapirs' core areas of use at both the 50% (48%) and 25% (71%) levels. Agricultural and pastoral land, Low dense forest, and Temporary lakes were the least represented habitat types in the core areas of use of tapirs in the southeast border. Riparian forest along the Paranapanema River was the most represented habitat type within tapir home ranges in both dry and wet seasons (Table 5.2).

Four habitat types were found within the home ranges and core areas of use of tapirs radio-tracked in the centre of Morro do Diabo (Table 5.1). The most represented habitat type in tapir home ranges in the centre was Tall mature forest (63%). Likewise, Tall mature forest was the most strongly represented habitat type in the tapirs' core areas of use at both the 50% (68%) and 25% (73%) levels. Secondary forest in early stages of regeneration and Low dense forest were the least represented habitat types in the core areas of use of tapirs in the centre. Tall mature forest was the most represented habitat type within tapir home ranges in both dry and wet seasons (Table 5.2). It is important to mention that the two main permanent water courses that run through the central area of Morro do Diabo - Onça and Taquara streams - are located within patches of Tall mature forest.

Six habitat types were found within the home ranges and core areas of use of tapirs radio-tracked in the north western border of Morro do Diabo (Table 5.1). The most represented habitat type in tapir home ranges in the north western border was Tall mature forest (48%). Likewise, Tall mature forest was the most strongly represented habitat type in the tapirs' core areas of use at both the 50% (53%) and 25% (54%) levels. Agricultural and pastoral land, Low mature forest, and Low dense forest were the least represented habitat types in the core areas of use of tapirs in the northwest border. Tall mature forest was the most represented habitat type within tapir home ranges in the wet season (52%), while Secondary forest in late stages of regeneration was the most represented habitat type (39%) in the dry season (Table 5.2).

Table 5.1. Percentage of each habitat type within the home range (HR, KDE95%) and core areas of use (CA KDE50%, CA KDE25%) of 19 lowland tapirs radio-tracked in four different sections of Morro do Diabo State Park, São Paulo, Brazil. (N=number of tapirs; TMF: Tall mature forest; LMF: Low mature forest; SFESR: Secondary forest in early stages of regeneration; SFLSR: Secondary forest in late stages of regeneration; RFRB: Riparian forest along the Ribeirão Bonito stream; RFPR: Riparian forest along the Paranapanema River; LDFV: Low, dense forest in various stages of regeneration; TL: Temporary lakes; AGPL: Agriculture/pasture).

West Border (N=7)

Habitat Type	HR KDE95%	Habitat Type	CA KDE50%	Habitat Type	CA KDE25%
TMF	33.4	**TMF**	29.8	**RFRB**	45.2
AGPL	16.2	**RFRB**	28.9	**TMF**	19.6
LMF	13.6	**LDFV**	12.0	**LDFV**	11.8
RFRB	10.6	**LMF**	11.9	**LMF**	9.6
SFLSR	9.5	**SFESR**	9.5	**SFESR**	7.5
LDFV	8.7	**AGPL**	5.5	**AGPL**	5.4
SFESR	8.2	**SFLSR**	2.6	**SFLSR**	0.9

Southeast Border (N=3)

Habitat Type	HR KDE95%	Habitat Type	CA KDE50%	Habitat Type	CA KDE25%
RFPR	31.1	**RFPR**	48.3	**RFPR**	71.0
TMF	29.9	**SFLSR**	21.0	**SFLSR**	12.3
SFLSR	18.7	**SFESR**	12.0	**TMF**	6.6
AGPL	11.8	**TMF**	11.0	**SFESR**	4.9
SFESR	6.3	**AGPL**	4.6	**AGPL**	4.7
TL	2.0	**TL**	1.8	**LDFV**	0.5
LDFV	0.4	**LDFV**	1.1	**TL**	0

Centre (N=7)

Habitat Type	HR KDE95%	Habitat Type	CA KDE50%	Habitat Type	CA KDE25%
TMF	62.6	**TMF**	67.7	**TMF**	73.3
SFLSR	35.5	**SFLSR**	31.2	**SFLSR**	24.8
SFESR	1.3	**SFESR**	1.0	**SFESR**	1.8
LDFV	0.5	**LDFV**	0.1	**LDFV**	0

Northwest Border (N=2)

Habitat Type	HR KDE95%	Habitat Type	CA KDE50%	Habitat Type	CA KDE25%
TMF	48.2	**TMF**	53.3	**TMF**	54.0
SFLSR	27.3	**SFLSR**	28.5	**SFLSR**	33.3
AGPL	11.5	**SFESR**	11.6	**SFESR**	12.2
SFESR	11.0	**AGPL**	4.9	**LDFV**	0.3
LMF	1.8	**LMF**	1.5	**AGPL**	0.1
LDFV	0.1	**LDFV**	0.1	**LMF**	0

Table 5.2. Percentage of each habitat type within the home range (HR, KDE95%) used in dry and wet seasons by 14 lowland tapirs radio-tracked in four different sections of Morro do Diabo State Park, São Paulo, Brazil. (N=number of tapirs; TMF: Tall mature forest; LMF: Low mature forest; SFESR: Secondary forest in early stages of regeneration; SFLSR: Secondary forest in late stages of regeneration; RFRB: Riparian forest along the Ribeirão Bonito stream; RFPR: Riparian forest along the Paranapanema River; LDFV: Low, dense forest in various stages of regeneration; TL: Temporary lakes; AGPL: Agriculture/pasture).

West Border (N=4)

Habitat Type	HR-Dry KDE95%	Habitat Type	HR-Wet KDE95%
TMF	39.5	**TMF**	34.6
AGPL	13.5	**AGPL**	14.8
SFLSR	11.8	**SFLSR**	13.0
RFRB	10.9	**RFRB**	12.1
LMF	10.1	**LMF**	11.9
LDFV	7.3	**LDFV**	6.9
SFESR	6.9	**SFESR**	6.7

Southeast Border (N=3)

Habitat Type	HR-Dry KDE95%	Habitat Type	HR-Wet KDE95%
RFPR	31.9	**RFPR**	30.1
TMF	27.1	**TMF**	28.9
SFLSR	20.5	**SFLSR**	24.8
AGPL	11.0	**AGPL**	7.8
SFESR	6.5	**SFESR**	6.4
TL	2.6	**TL**	1.3
LDFV	0.4	**LDFV**	0.6

Centre (N=6)

Habitat Type	HR-Dry KDE95%	Habitat Type	HR-Wet KDE95%
TMF	63.8	**TMF**	68.2
SFLSR	34.2	**SFLSR**	30.4
SFESR	1.2	**SFESR**	1.2
LDFV	0.7	**LDFV**	0.2

Northwest Border (N=1)

Habitat Type	HR-Dry KDE95%	Habitat Type	HR-Wet KDE95%
SFLSR	39.2	**TMF**	52.1
TMF	28.1	**SFLSR**	44.8
AGPL	17.2	**LMF**	3.1
SFESR	10.9	**AGPL**	0
LMF	4.5	**SFESR**	0
LDFV	0	**LDFV**	0

5.3.2 Tapir Habitat Selection

5.3.2.1 Habitat Availability and Habitat Use

The total areas available to radio-tracked tapirs in each section of Morro do Diabo are presented in Table 5.3.

Table 5.3. Total area available (km²) for 19 lowland tapirs radio-tracked in four different sections of Morro do Diabo State Park (MDSP), São Paulo, Brazil. Total area used by tapirs in each section (KDE95%, km²) and ½MMDM values used to calculate areas available are shown. (N=number of tapirs; MMDM=Mean Maximum Distance Moved).

Area MDSP	N	Area Used (KDE95%) (km²)	½MMDM (km)	Area Available (KDE95%+Buffer) (km²)
West Border	7	24	2.0	92
Southeast Border	3	4	0.9	16
Centre	7	16	1.7	74
Northwest Border	2	13	1.1	32

Eight habitat types were available to tapirs radio-tracked in the western border of Morro do Diabo (Table 5.4). Tall mature forest had the highest percentage of use (30%), closely followed by Riparian forest along the Ribeirão Bonito stream (25%). Likewise, Tall mature forest had the highest percentage of use in both dry (31%) and wet (28%) seasons.

Seven habitat types were available to tapirs radio-tracked in the south eastern border of Morro do Diabo (Table 5.4). Riparian forest along the Paranapanema River had the highest percentage of use (49%). Likewise, Riparian forest along the Paranapanema River had the highest percentage of use in both dry (47%) and wet (50%) seasons.

Five habitat types were available to tapirs radio-tracked in the centre of Morro do Diabo (Table 5.4). Tall mature forest had the highest percentage of use (73%). Likewise, Tall mature forest had the highest percentage of use when analysing the data separately for dry (70%) and wet (78%) seasons.

Six habitat types were available to tapirs radio-tracked in the north western border of Morro do Diabo (Table 5.4). Tall mature forest had the highest percentage of use (46%), closely followed by Secondary forest in late stages of regeneration (44%). Secondary forest in late stages of regeneration had the highest percentage of use in the dry season (54%), while Tall mature forest had the highest percentage of use in the wet season (56%).

Table 5.4. Habitat availability (km² and %) and habitat use (%) in the home range of 19 lowland tapirs radio-tracked in four different sections of Morro do Diabo State Park, São Paulo, Brazil. Habitat use in wet and dry seasons is shown. (N=number of tapirs; *Maximum; **Minimum; TMF: Tall mature forest; LMF: Low mature forest; SFESR: Secondary forest in early stages of regeneration; SFLSR: Secondary forest in late stages of regeneration; RFRB: Riparian forest along the Ribeirão Bonito stream; RFPR: Riparian forest along the Paranapanema River; LDFV: Low, dense forest in various stages of regeneration; TL: Temporary lakes; AGPL: Agriculture/pasture).

West Border (N=7)

Habitat Type	Habitat Availability (km²)	Habitat Availability (%)	Habitat Use Home Range (%)	Habitat Use Wet Season (%)	Habitat Use Dry Season (%)
AGPL	37.6	41.1	4.9	5.1	4.6
TMF	30.6	33.4	**29.6***	**28.0***	**31.2***
SFLSR	7.8	8.5	9.1	10.6	7.6
LMF	5.5	6.0	10.3	9.8	10.8
SFESR	4.0	4.3	10.7	9.0	12.5
LDFV	3.2	3.5	10.2	10.8	9.5
RFRB	2.9	3.1	25.2	26.6	23.8
TL	0	0	**0****	**0****	**0****

Southeast Border (N=3)

Habitat Type	Habitat Availability (km²)	Habitat Availability (%)	Habitat Use Home Range (%)	Habitat Use Wet Season (%)	Habitat Use Dry Season (%)
AGPL	6.2	38.1	4.4	4.8	3.9
TMF	4.0	24.7	18.9	19.0	18.7
SFLSR	2.0	12.4	15.8	14.9	16.8
RFPR	1.8	11.0	**48.7***	**50.2***	**46.9***
SFESR	1.3	8.0	8.9	7.9	10.2
TL	0.9	5.5	2.8	2.5	3.1
LDFV	0	0.2	**0.5****	**0.6****	**0.4****

Centre (N=7)

Habitat Type	Habitat Availability (km²)	Habitat Availability (%)	Habitat Use Home Range (%)	Habitat Use Wet Season (%)	Habitat Use Dry Season (%)
TMF	42.9	57.6	**72.6***	**78.2***	**69.7***
SFLSR	20.3	27.3	25.1	20.3	27.6
AGPL	5.6	7.5	**0****	**0****	**0****
SFESR	3.9	5.2	2.0	1.5	2.2
LDFV	1.8	2.4	0.3	**0****	0.4

Northwest Border (N=2)

Habitat Type	Habitat Availability (km²)	Habitat Availability (%)	Habitat Use Home Range (%)	Habitat Use Wet Season (%)	Habitat Use Dry Season (%)
TMF	11.2	35.0	**46.1***	**56.5***	30.4
AGPL	8.5	26.4	2.6	**0****	6.5
SFLSR	6.5	20.3	44.3	37.7	**54.3***
SFESR	4.7	14.7	4.3	4.3	4.3
LMF	1.0	3.1	2.6	1.4	4.3
LDFV	0.1	0.4	**0****	**0****	**0****

5.3.2.2 Habitat Selection Index

In the western border of Morro do Diabo, tapirs selected Riparian forest along the Ribeirão Bonito stream (Wi>1; P<Bonferroni level 0.00625). Agricultural and pastoral land was avoided (Wi<1; P<Bonferroni level 0.00625). Riparian forest along the Ribeirão Bonito stream was selected in both wet and dry seasons (Table 5.5).

In the south eastern border of Morro do Diabo, tapirs selected Riparian forest along the Paranapanema River was selected (Wi>1; P<Bonferroni level 0.00714). Agricultural and pastoral land was avoided (Wi<1; P<Bonferroni level 0.00714). Riparian forest along the Paranapanema River was selected in both wet and dry seasons (Table 5.5).

In the centre of Morro do Diabo, tapirs selected Tall mature forest (Wi>1; P<Bonferroni level 0.01). Agricultural and pastoral land and Low dense forest were avoided (Wi<1; P<Bonferroni level 0.01). Tall mature forest was selected in both wet and dry seasons. Agricultural and pastoral land, Secondary forest in early stages of regeneration, and Low dense forest were avoided in the wet season. Agricultural and pastoral land and Low dense forest were avoided in the dry season (Table 5.5).

In the north western border of Morro do Diabo, tapirs selected Secondary forest in late stages of regeneration (Wi>1; P< Bonferroni level 0.00833). Agricultural and pastoral land, Secondary forest in early stages of regeneration, and Low dense forest were avoided (Wi<1; P<Bonferroni level 0.00833). In the wet season, Tall mature forest and Secondary forest in late stages of regeneration were selected, while Agricultural and pastoral land, Secondary forest in early stages of regeneration, and Low dense forest were avoided. In the dry season, Secondary forest in late stages of regeneration was selected, while Agricultural and pastoral land, Secondary forest in early stages of regeneration, and Low dense forest were avoided (Table 5.5).

Table 5.5. Manly's standardised habitat selection index for 19 lowland tapirs radio-tracked in four different sections of Morro do Diabo State Park, São Paulo, Brazil. (N = number of tapirs; *Habitat type positively selected; **Habitat type significantly selected; ***Habitat type significantly avoided; TMF: Tall mature forest; LMF: Low mature forest; SFESR: Secondary forest in early stages of regeneration; SFLSR: Secondary forest in late stages of regeneration; RFRB: Riparian forest along the Ribeirão Bonito stream; RFPR: Riparian forest along the Paranapanema River; LDFV: Low, dense forest in various stages of regeneration; TL: Temporary lakes; AGPL: Agriculture/pasture).

West Border (N=7)

Habitat Type	Habitat Used	Habitat Available	Selection Index Wi	P (0.00625)
AGPL	0.05	0.41	0.118	**0.000*****
TMF	0.30	0.33	0.887	0.407
SFLSR	0.09	0.08	**1.069***	0.838
LMF	0.10	0.06	**1.709***	0.160
SFESR	0.11	0.04	**2.488***	0.038
LDFV	0.10	0.03	**2.942***	0.026
RFRB	0.25	0.03	**8.043***	**0.000****
TL	0.00	0.00	0.000	0.000

Southeast Border (N=3)

Habitat Type	Habitat Used	Habitat Available	Selection Index Wi	P (0.00714)
AGPL	0.04	0.38	0.115	**0.000*****
TMF	0.19	0.25	0.764	0.137
SFLSR	0.16	0.12	**1.268***	0.360
RFPR	0.49	0.11	**4.416***	**0.000****
SFESR	0.09	0.08	**1.112***	0.752
TL	0.03	0.05	0.513	0.108
LDFV	0.01	0.00	**2.206***	0.691

Centre (N=7)

Habitat Type	Habitat Used	Habitat Available	Selection Index Wi	P (0.01)
TMF	0.73	0.58	**1.261***	**0.001****
SFLSR	0.25	0.27	0.920	0.616
AGPL	0.00	0.07	0.000	**0.000*****
SFESR	0.02	0.05	0.374	0.018
LDFV	0.00	0.02	0.119	**0.000*****

Northwest Border (N=2)

Habitat Type	Habitat Used	Habitat Available	Selection Index Wi	P (0.00833)
TMF	0.46	0.35	**1.316***	0.027
AGPL	0.03	0.26	0.099	**0.000*****
SFLSR	0.44	0.20	**2.181***	**0.000****
SFESR	0.04	0.15	0.295	**0.000*****
LMF	0.03	0.03	0.845	0.764
LDFV	0.00	0.00	0.000	**0.000*****

5.3.3 Tapir Activity Patterns

The study of tapir activity patterns in Morro do Diabo shows that tapirs rest during the day and begin their activity after sunset. The main periods of activity of the 19 tapirs radio-tracked during this study were from 19:00-24:00 h, with a peak between 20:00-21:00 h (63% active), and from 01:00-07:00 h, with a peak between 05:00-06:00 h (60%). Tapirs were largely inactive from 11:00-16:00 h, with the lowest percentage of activity between 12:00-13:00 h (25%) (Figure 5.1).

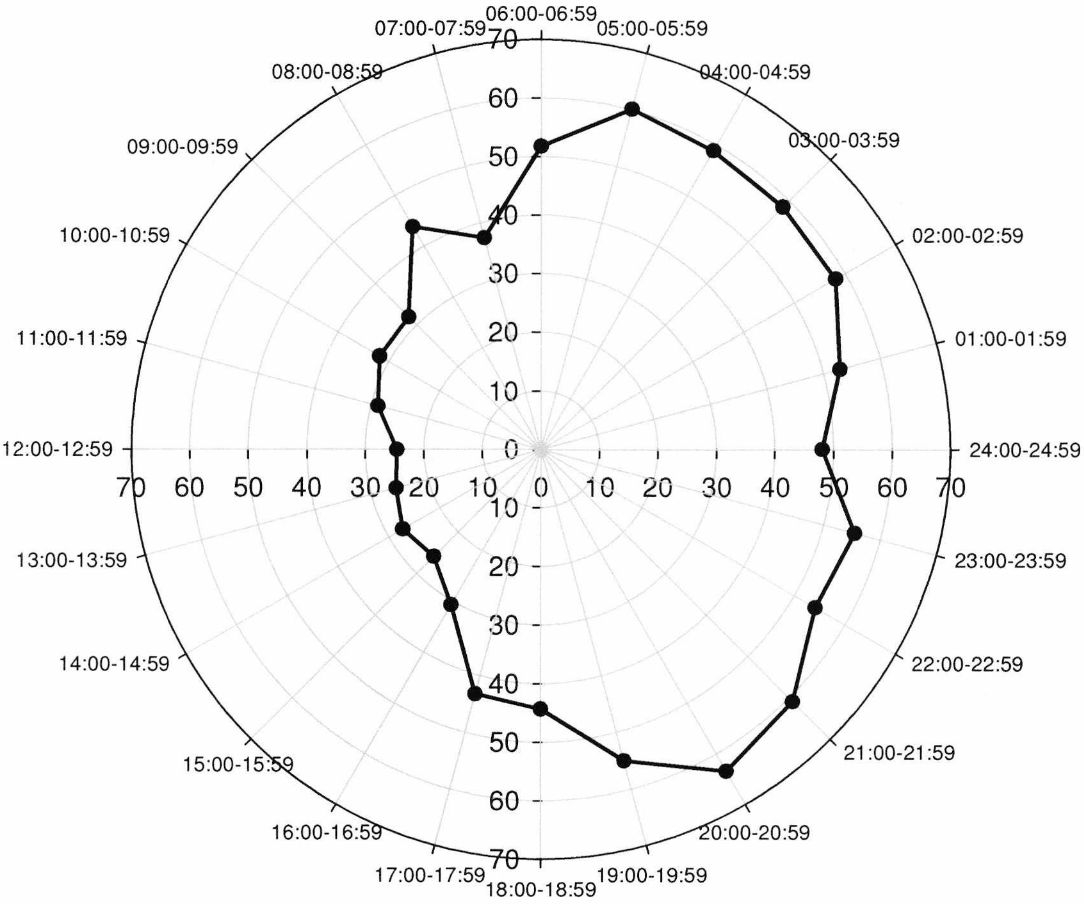


Figure 5.1. Mean percentages of active locations of 19 lowland tapirs radio-tracked in Morro do Diabo State Park, São Paulo, Brazil.

5.3.3.1 Activity Patterns in Different Seasons

In the wet season, the main period of tapir activity was from 19:00-06:00 h, including two peaks: 20:00-21:00 h (65% active) and 05:00-06:00 h (66%). The main peak of inactivity was between 13:00-14:00 h (16%) (Figure 5.2). In the dry season, the main periods of activity were from 19:00-24:00 h, with a peak between 20:00-21:00 h (62%), and from 02:00-07:00 h, with a peak between 02:00-03:00 h (60%). The main peak of inactivity in the dry season was between 12:00-13:00 h (22%) (Figure 5.3).

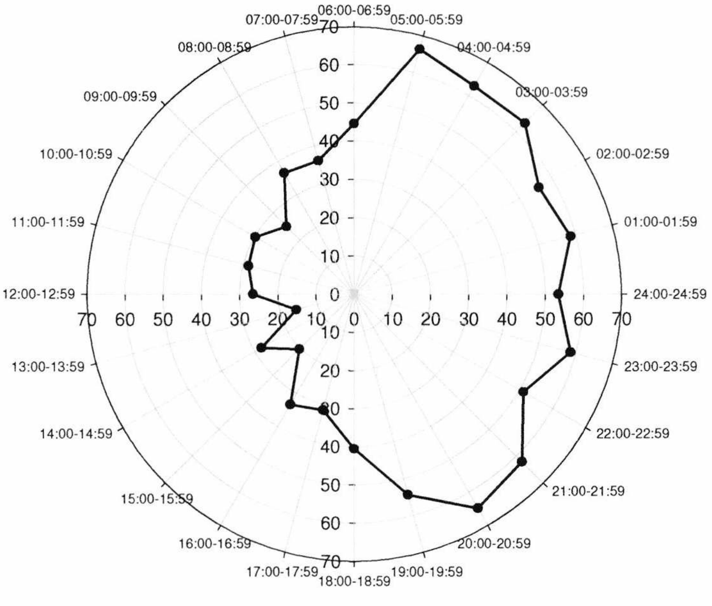


Figure 5.2. Mean percentages of active locations of 19 lowland tapirs radio-tracked in periods of WET season in Morro do Diabo State Park, São Paulo, Brazil.

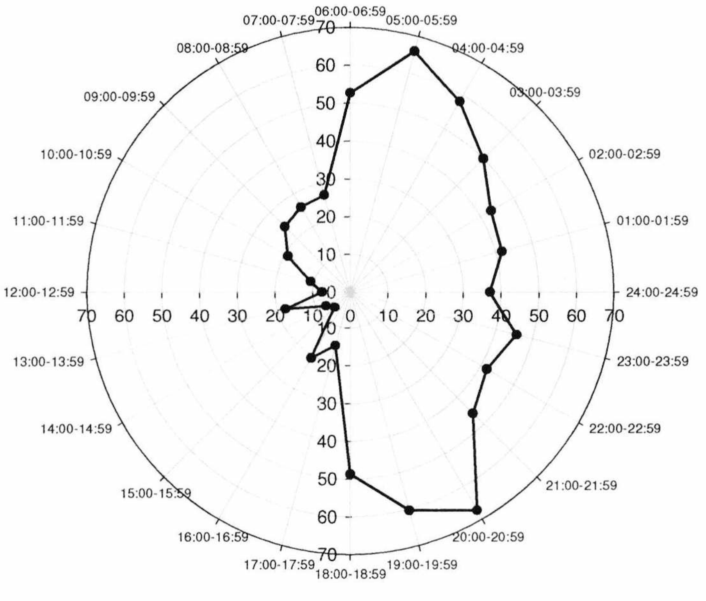


Figure 5.3. Mean percentages of active locations of 19 lowland tapirs radio-tracked in periods of DRY season in Morro do Diabo State Park, São Paulo, Brazil.

5.3.3.2 Activity Patterns of Different Sexes

The main period of activity of female tapirs was from 19:00-07:00 h, including two peaks: 20:00-21:00 h (66% active) and 05:00-06:00 h (64%). Females were largely inactive from 12:00-16:00 h, with the lowest percentage of activity between 15:00-16:00 h (25%) (Figure 5.4). The main peaks of activity of male tapirs were: 21:00-22:00 h (56%) and 08:00-09:00 h (59%). Males were largely inactive from 10:00-13:00 h, with 0 active locations between 11:00-12:00 h (Figure 5.5).

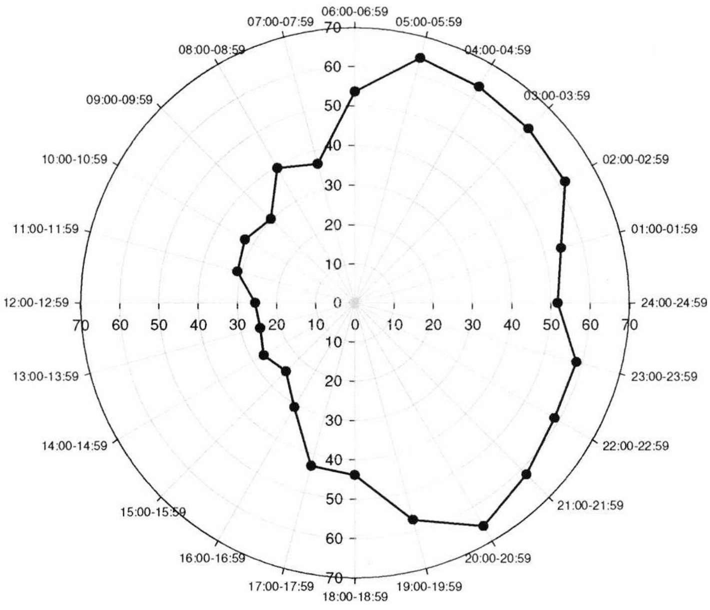


Figure 5.4. Mean percentages of active locations of 13 FEMALE lowland tapirs radio-tracked in Morro do Diabo State Park, São Paulo, Brazil.

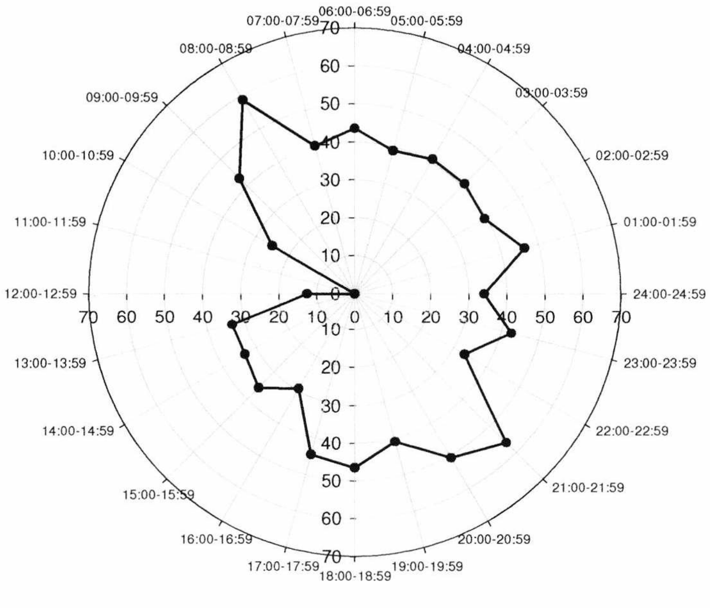


Figure 5.5. Mean percentages of active locations of 6 MALE lowland tapirs radio-tracked in Morro do Diabo State Park, São Paulo, Brazil.

5.3.3.3 Activity Patterns of Different Age Classes

The main period of activity of adult tapirs was from 19:00-07:00 h, including two peaks: 21:00-22:00 h (65% active) and 03:00-04:00 h (61%). The main peak of inactivity for adults was between 13:00-14:00 h (25%) (Figure 5.6). The main periods of activity of sub-adult tapirs were from 19:00-21:00 h, with a peak between 20:00-21:00 h (67%), and from 03:00-07:00 h, with a peak between 05:00-06:00 h (66%). Sub-adults were largely inactive from 12:00-16:00 h, with the lowest activity between 15:00-16:00 h (6%) (Figure 5.7).

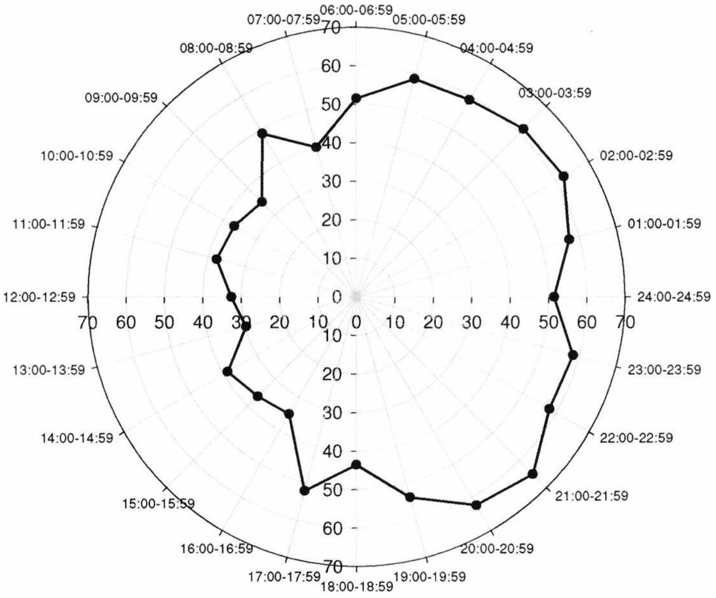


Figure 5.6. Mean percentages of active locations of 15 ADULT lowland tapirs radio-tracked in Morro do Diabo State Park, São Paulo, Brazil.

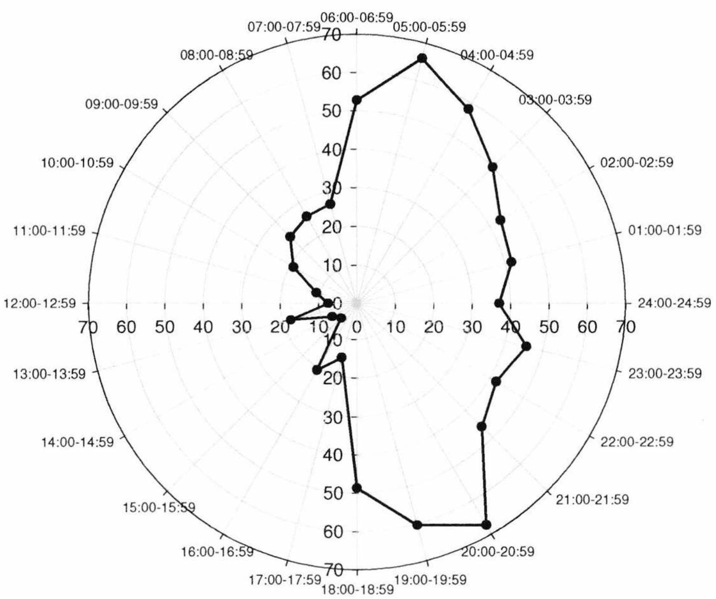


Figure 5.7. Mean percentages of active locations of 4 SUB-ADULT lowland tapirs radio-tracked in Morro do Diabo State Park, São Paulo, Brazil.

5.3.4 Patterns of Tapir Habitat Use in Relation to Activity

In the western border of Morro do Diabo, tapirs spent the highest percentage of their active time (29%) in Tall mature forest, closely followed by Riparian forest along the Ribeirão Bonito stream (24%). The same habitat types presented the highest percentages of inactive time: Tall mature forest (27%) and Riparian forest along the Ribeirão Bonito stream (22%). Therefore, these seemed to be the habitat types where tapirs travelled, foraged, and rested in the western border. The same patterns were observed when looking at percentages of active and inactive time separately for wet and dry seasons (Table 5.6).

In the south eastern border of Morro do Diabo, tapirs spent 51% of their active time and 45% of their inactive time in Riparian forest along the Paranapanema River. Therefore, this seemed to be the habitat type where tapirs travelled, foraged, and rested in the south eastern border. The same patterns were observed when looking at percentages of active and inactive time separately for wet and dry seasons (Table 5.6).

In the centre of Morro do Diabo, tapirs spent 71% of their active time and 74% of their inactive time in Tall mature forest. In both cases, Secondary forest in late stages of regeneration came in second place. Tall mature forest was by far the habitat type in the centre of Morro do Diabo where tapirs performed most of their travelling, foraging, and resting activities. The same patterns were observed when looking at percentages of active and inactive time separately for wet and dry seasons (Table 5.6).

In the north western border of Morro do Diabo, tapirs spent 49% of their active time in Tall mature forest, followed by 38% in Secondary forest in late stages of regeneration. Secondary forest in late stages of regeneration had the highest percentage of inactive time (53%). In the wet season, tapirs in the north western border spent the highest percentage of their active time (63%) in Tall mature forest, while in the dry season they spent 49% of their active time in Secondary forests in late stages of regeneration (Table 5.6).

Table 5.6. Percentages of tapir activity and inactivity in different habitat types in four sections of Morro do Diabo State Park, São Paulo, Brazil. Results for all tapir locations within their home ranges, as well as in wet and dry seasons are shown. (%ACT=% active; %INA=% inactive; TMF: Tall mature forest; LMF: Low mature forest; SFESR: Secondary forest in early stages of regeneration; SFLSR: Secondary forest in late stages of regeneration; RFRB: Riparian forest along the Ribeirão Bonito stream; RFPR: Riparian forest along the Paranapanema River; LDFV: Low, dense forest in various stages of regeneration; TL: Temporary lakes; AGPL: Agriculture/pasture).

West Border					
Home Range		**Wet Season**		**Dry Season**	
Habitat Type	**%ACT**	**Habitat Type**	**%ACT**	**Habitat Type**	**%ACT**
TMF	29.3	**TMF**	27.4	**TMF**	31.0
RFRB	24.5	**RFRB**	25.3	**RFRB**	23.8
SFESR	11.7	**LDFV**	11.7	**SFESR**	13.0
LDFV	10.3	**SFESR**	10.2	**LMF**	9.6
SFLSR	9.4	**SFLSR**	9.9	**LDFV**	9.1
LMF	9.2	**LMF**	8.8	**SFLSR**	9.0
AGPL	5.5	**AGPL**	6.7	**AGPL**	4.5
Habitat Type	**%INA**	**Habitat Type**	**%INA**	**Habitat Type**	**%INA**
TMF	26.7	**RFRB**	25.4	**TMF**	29.0
RFRB	22.5	**TMF**	24.7	**RFRB**	19.4
LMF	14.7	**LMF**	13.6	**LMF**	15.9
LDFV	12.0	**SFESR**	10.9	**LDFV**	13.6
SFESR	10.8	**LDFV**	10.7	**SFESR**	10.6
AGPL	8.1	**AGPL**	8.2	**AGPL**	8.0
SFLSR	5.1	**SFLSR**	6.6	**SFLSR**	3.6
Southeast Border					
Home Range		**Wet Season**		**Dry Season**	
Habitat Type	**%ACT**	**Habitat Type**	**%ACT**	**Habitat Type**	**%ACT**
RFPR	51.4	**RFPR**	51.6	**RFPR**	51.1
TMF	17.5	**TMF**	16.8	**TMF**	18.3
SFLSR	15.1	**SFLSR**	16.0	**SFLSR**	14.1
SFESR	7.6	**SFESR**	7.4	**SFESR**	7.8
AGPL	4.1	**AGPL**	4.5	**TL**	4.1
TL	3.7	**TL**	3.3	**AGPL**	3.6
LDFV	0.6	**LDFV**	0.4	**LDFV**	0.9
Habitat Type	**%INA**	**Habitat Type**	**%INA**	**Habitat Type**	**%INA**
RFPR	45.5	**RFPR**	48.4	**RFPR**	41.7
TMF	19.6	**TMF**	22.0	**SFLSR**	26.0
SFLSR	17.5	**SFESR**	12.7	**TMF**	16.6
SFESR	11.7	**SFLSR**	11.0	**SFESR**	10.3
AGPL	3.5	**AGPL**	3.1	**AGPL**	4.0
LDFV	1.4	**LDFV**	2.4	**TL**	1.3
TL	0.8	**TL**	0.3	**LDFV**	0.0
Centre					
Home Range		**Wet Season**		**Dry Season**	
Habitat Type	**%ACT**	**Habitat Type**	**%ACT**	**Habitat Type**	**%ACT**
TMF	70.9	**TMF**	77.5	**TMF**	67.0
SFLSR	28.3	**SFLSR**	22.5	**SFLSR**	31.7
SFESR	0.6	**SFESR**	0.0	**SFESR**	1.0
LDFV	0.2	**LDFV**	0.0	**LDFV**	0.2
Habitat Type	**%INA**	**Habitat Type**	**%INA**	**Habitat Type**	**%INA**
TMF	73.9	**TMF**	78.0	**TMF**	71.8
SFLSR	23.2	**SFLSR**	19.6	**SFLSR**	25.1
SFESR	2.6	**SFESR**	2.3	**SFESR**	2.7
LDFV	0.3	**LDFV**	0.0	**LDFV**	0.4

Northwest Border					
Home Range		Wet Season		Dry Season	
Habitat Type	**%ACT**	**Habitat Type**	**%ACT**	**Habitat Type**	**%ACT**
TMF	48.9	**TMF**	62.7	**SFLSR**	48.8
SFLSR	38.0	**SFLSR**	29.4	**TMF**	31.7
SFESR	5.4	**SFESR**	3.9	**SFESR**	7.3
LMF	4.3	**LMF**	3.9	**AGPL**	7.3
AGPL	3.3	**AGPL**	0.0	**LMF**	4.9
Habitat Type	**%INA**	**Habitat Type**	**%INA**	**Habitat Type**	**%INA**
SFLSR	52.9	**TMF**	48.0	**SFLSR**	66.7
TMF	44.1	**SFLSR**	48.0	**TMF**	33.3
SFESR	2.9	**SFESR**	4.0	**SFESR**	0.0
AGPL	0.0	**AGPL**	0.0	**AGPL**	0.0
LMF	0.0	**LMF**	0.0	**LMF**	0.0

5.4 Discussion

5.4.1 Spatial Interactions between Lowland Tapirs and the Landscape

5.4.1.1 Habitat Composition in Tapir Home Ranges and Core Areas of Use

Overall, tapirs in Morro do Diabo incorporated varying portions of all available habitat types within their home ranges and core areas of use. Tall mature forest was the habitat type most largely represented in tapir home ranges. Riparian environments were the most strongly represented habitats in core areas of use. These included the forests along the Ribeirão Bonito stream in the western limit of Morro do Diabo, the forests along the Paranapanema River along the southern limit, and some patches of Tall mature forest in the centre of Morro do Diabo. The two main permanent water courses that run through the central area of Morro do Diabo - Onça and Taquara streams - are located within patches of Tall mature forest. Secondary forest habitats, found in Morro do Diabo in various stages of regeneration, were, in most cases, the least represented habitats within the home ranges and core areas of use of tapirs in Morro do Diabo. All these patterns showed very little seasonal variation.

Interestingly, the second most strongly represented habitat type within the home ranges of tapirs in the western border of Morro do Diabo was agricultural and pastoral land (16%), a pattern that was also observed when running separate analyses for different seasons. This result might be explained by the fact that two of the tapirs radio-tracked in the western border left the boundaries of Morro do Diabo and crossed the agricultural and pasture land matrix in order to reach another forest fragment nearby (Chapter 3). In fact, one of these radio-collared tapirs, a sub-adult female (Chu-Chu), had the largest home range size of all 19 tapirs radio-tracked during this study (14.2 km^2, KDE95%), and her home range area included a high percentage of the agricultural and pastoral land habitat type (Chapter 3, Figure 3.5.1). At any rate, while these tapir movements through agricultural and pastoral land were fairly frequent, this habitat type was the least represented in the core areas of use of these tapirs, which were in effect located inside Morro do Diabo (Chapter 3, Figures 3.5.1 and 3.5.2). Indeed, the agricultural and pastoral land habitat was overall scantily represented in the core areas of use of tapirs in all sections of Morro do Diabo. This provided indication that tapirs crossed these areas of agricultural crops and cattle ranching while travelling in between forest fragments, but did not necessarily use the landscape matrix for their main activities such as foraging and resting.

5.4.1.2 Tapir Habitat Use and Habitat Selection

Overall, tapirs in Morro do Diabo used most of the habitat types available to them to varying degrees. Tall mature forest was by far the most used habitat type by tapirs. The only exception to this occurred in the south eastern border of Morro do Diabo where the most used habitat was Riparian forests along the Paranapanema River. The least used habitat types in Morro do Diabo were Agricultural and pastoral land, Temporary lakes, and Low dense forests. Very little seasonal variation in habitat use was observed. The same was observed for lowland tapirs in Lago Caiman, Bolivia, where no seasonal variation in track encounter rates in different habitat types was found (Herrera *et al.* 1999). In contrast, Salas (1996) found seasonal variations in lowland tapir habitat use in the Tabaro River Valley in Venezuela, with tapirs using different habitats in different seasons in order to search for and ingest more fruit in season. Ayala (2003) also observed that lowland tapirs in Kaa-Iya del Gran Chaco National Park, Bolivia, did use different habitat types in different seasons.

Habitat use by lowland tapirs in Morro do Diabo was not as predicted by habitat availability. While tapirs in Morro do Diabo used most of the available habitat types, they showed strong patterns of habitat selection and habitat avoidance. In three out of four sections of Morro do Diabo, tapirs strongly selected riparian habitats during both seasons. In the western border, tapirs significantly selected the riparian forests along the Ribeirão Bonito stream. This stream runs along the entire western edge of Morro do Diabo and is the most important source of water for wildlife in that area. The vegetation along the stream is characterised by several islands of swamp vegetation and patches of humid fields, both surrounded by riparian forests. In the south eastern border, tapirs significantly selected the riparian forests along the Paranapanema River, the major permanent source of water in Morro do Diabo. In the centre of Morro do Diabo, tapirs significantly selected tall mature forest. The two main permanent water courses that run through the central part of Morro do Diabo are located in patches of tall mature forests therefore providing another evidence of tapir selection of riparian habitats. The only exception to this pattern was observed in the north western border of Morro do Diabo, where tapirs significantly selected secondary forests in late stages of regeneration, where no permanent water courses were found.

The strong selection of riparian environments corroborated the previous finding of this study that riparian habitats are highly represented in the tapir core areas of use in Morro do Diabo. This provides evidence that tapirs not only select riparian habitats, but they establish their main core areas of use in these habitats. This may be because the riparian forests along the permanent water courses in Morro do Diabo are the most diverse and abundant in food resources for wildlife (Faria & Pires 2006). Moreover, tapirs are known to be closely associated with riparian forests, marshes, lakes and streams all throughout their distribution ranges

(Padilla & Dowler 1994; Medici 2001). In the Peruvian Amazon, Bodmer (1990b) observed that lowland tapirs select moist forests such as floodplains. Naranjo (1995) found that Baird's tapir sign in Corcovado National Park, Costa Rica, was positively correlated with distance from perennial water bodies. Among the habitat types preferred by Baird's tapirs in the Lacandon Forest, Mexico, were palm swamps and riparian forests (Muench 2001). Naranjo (2009) noted that Baird's tapirs prefer habitats that include great availability of permanent water bodies and large extensions of riparian vegetation.

Overall, tapirs in Morro do Diabo showed very little use and in some cases avoidance of areas of secondary growth. Secondary forests in early stages of regeneration were significantly avoided by tapirs in the centre of Morro do Diabo during the dry season, while in the north western border this habitat type was significantly avoided in both seasons. This contradicts what has been observed by other tapir studies in different areas were secondary growth habitats were largely used and selected. In the Lacandon Forest, Mexico, Muench (2001) found that Baird's tapirs preferred secondary regeneration vegetation over mature forest. Likewise, evidence from Corcovado National Park, Costa Rica, and Montes Azules Biosphere Reserve, Mexico, showed that Baird's tapirs were more abundant in second-growth forests and palm swamps than in drier, higher areas (Naranjo 1995; Bolaños & Naranjo 2001; Foerster & Vaughan 2002; Naranjo & Bodmer 2002). Foerster & Vaughan (2002) observed that study-long habitat utilisation by Baird's tapirs in Corcovado National Park, Costa Rica, was not as predicted by habitat availability given that secondary forests were used more than expected while primary forests were used less than expected. Foerster & Vaughan (2002) also noted seasonal variations in habitat selection, which were correlated with fruit availability. Lizcano (2006) found that mountain tapirs in Los Nevados National Park, Colombia, selected secondary forests and avoided *páramos* and ecotones, and showed no preference for or against mature forests. The high levels of degradation of secondary growth habitats in Morro do Diabo may explain why tapirs did not select these areas. Most of the areas of secondary growth in Morro do Diabo originated from past and recurrent fire events. In addition, some of these patches originated during the construction of both the highway and the railway that crossed Morro do Diabo, and continue to suffer degradation from "edge effect". Overall, the secondary forests in Morro do Diabo have been largely invaded by grasses, lianas, and bamboo, and present very low quality in terms of providing food resources for wildlife.

Areas of agricultural and pastoral land were significantly avoided by tapirs in all four sections of Morro do Diabo where the study took place. This is another indication that tapirs cross these areas while travelling in between forest fragments, but do not necessarily use the landscape matrix outside Morro do Diabo for their main activities such as foraging and resting. Similar observations have been made in Southeast Asia, where Malayan tapirs have been recorded in agricultural areas (Williams & Pétrides 1980; Brooks *et al.* 1997). In Malaysia, there have been sporadic records of Malayan tapirs crossing areas of palm oil estates. This seemed to occur primarily due to lack of choice, as the animals travelled from one forested area to the next (C. Traeholt, personal communication). While the areas of agricultural and pastoral land around Morro do Diabo consist of an anthropogenic habitat type, tapir species in general appear to avoid open areas, even in natural environments. Desbiez (2009) applied diurnal line-transect sampling in the mosaic of natural habitat types found in the Pantanal and estimated higher densities of lowland tapirs in forest habitats, when compared to open grasslands and floodplains. Naranjo & Cruz-Aldán (1998) as well as Lira *et al.* (2004) noted that Baird's tapirs prefer densely forested areas, rather than opener, and more disturbed habitats. Downer (2001) noted that mountain tapirs rarely use open habitats (pampas) in the Andes, in spite of their considerable food value.

5.4.2 Temporal Interactions between Lowland Tapirs and the Landscape

5.4.2.1 Tapir Activity Patterns

As widely published in the available literature, tapirs are primarily nocturnal and crepuscular species. Large animals - such as tapirs - have a difficult time dissipating excess body heat due to their low surface to volume ratio (Schmidt-Nielsen 1990). Therefore, the nocturnal behaviour of tapirs may help with thermoregulation, with tapirs resting during the hot daytime, and confining their activities to the cooler night-time hours (Foerster & Vaughan 2002). This study has corroborated these previous findings and shows that tapirs rest during the day and begin their activity after sunset. Tapir activity in Morro do Diabo showed a very clear bimodal pattern, including two main peaks of activity, the first in the early hours of the evening from 20:00-21:00 h, and the second in the early hours of the day from 05:00-06:00 h. Overall, tapirs in Morro do Diabo foraged for ~5 hours in the early evening, and then rested for a few hours in the middle of the night, and then made a second foraging bout of ~6 hours in the early hours of the day.

Previous studies on lowland and mountain tapir activity patterns have obtained similar results. Tobler (2008) observed that the main peaks of lowland tapir activity in the Peruvian Amazon were from 19:00-20:00 h and from 03:00-04:00 h. Maffei *et al.* (2002) used camera-traps in the Chiquitano Forest, Bolivia, and noted that most lowland tapir pictures were taken from 24:00-08:00 h. Telemetry and camera-trapping studies of lowland tapirs in Kaa-Iya del Gran Chaco National Park, Bolivia, indicated that the main peak of tapir activity was from 01:00-06:30 h (Ayala 2003; Noss *et al.* 2003). Daily activity of mountain tapirs in Los Nevados National Park, Colombia, showed a bimodal pattern, with maxima during the early hours of the day (05:00-07:00 h) and early hours of the evening (18:00-20:00 h) (Lizcano & Cavelier 2000b). Lowland tapirs in Morro do Diabo were largely inactive in the middle of the day, from

11:00-16:00 h. The same was observed for lowland tapirs in Kaa-Iya del Gran Chaco National Park, Bolivia, where very little activity was observed from 11:00-15:30 h (Ayala 2002).

Padilla & Dowler (1994) noted that tapirs shelter themselves in forests and thickets during day hours. Tapirs in Morro do Diabo appeared to have defined shelters they used as resting sites. These locations were used repeatedly over long periods of time. The same was observed by Tobler (2008) in the Peruvian Amazon. In Morro do Diabo, tapirs rested at one site during most of the day but occasionally moved between different spots a few metres away from each other, most probably searching for shade. In addition, tapirs in Morro do Diabo rested during day time in areas different from those they used for foraging at night, and daily movements between resting and feeding sites resulted in well-worn paths. In fact, the observed peaks of tapir activity in Morro do Diabo most probably corresponded to tapirs moving between resting and foraging areas. Tobler (2008) observed very little overlap and low similarity between day time and night time lowland tapir home ranges.

Tapir activity patterns analysed separately for wet and dry seasons, as well for both sexes and different age classes in Morro do Diabo were fairly consistent. They presented two main peaks of activity, one in the early hours of the evening and a second one in the early hours of the morning. However, a few variations on the patterns were observed. First, during the wet season, tapirs did not seem to rest at all during the night and were active for ~11 hours, from 19:00-06:00 h. In addition, tapirs rested more during the day. Ayala (2003) found a similar pattern in Kaa-Iya National Park, Bolivia, were lowland tapirs were more active during the night during the wet season, which was explained by the highest availability of food resources in the Bolivian Chaco during the wet season. Availability of food resources does not seem to explain the higher levels of nocturnal tapir activity during the wet season in Morro do Diabo. In the semi-deciduous forests of the Atlantic Forest of the Interior the availability of fruit is not related to rainfall, with most of the plant species fruiting during the middle and end of the dry season and at the beginning of the wet season (Valladares-Padua 1993). Therefore, the higher nocturnal tapir activity during the wet season must be due to the fact that the highest annual temperatures in the Pontal do Paranapanema Region occur in the wet season. During the night, temperatures are considerably lower.

An interesting aspect of the activity patterns of tapirs in Morro do Diabo is that, female tapirs overall tended to be more active than males. Females were more active during crepuscular and night times, and for longer periods of time (~12 hours), than males. Female tapirs did not seem to rest at all during the night. In some cases, this might be related to the fact that females lactating and caring for a young calf may need to forage more in order to fulfil nutritional requirements. Ayala (2003) found a different pattern in the Bolivian Chaco, where male tapirs presented higher percentages of activity during the night than females. In terms of different age classes, adult tapirs in Morro do Diabo tended to be largely more active than sub-adults. While adult tapirs were greatly active for ~12 hours during crepuscular and night times, sub-adults made shorter bouts of activity in the early hours of the evening (~2 hours) and early hours of the day (roughly 4 hours). Adult tapirs did not seem to rest at all during the night, while sub-adults tended to take long breaks. Additionally, sub-adult tapirs rested for longer periods of time during day hours. Discussions about differences in activity patterns between the sexes and between age classes might be limited by the fact that the sample included small numbers of males (N=6) and sub-adults (N=4).

The results of tapir activity patterns obtained by radio-telemetry coincided with some general observations obtained by nocturnal line-transect sampling in Morro do Diabo (Chapter 4). Line-transect sampling was carried out from 18:00-23:00 h and resulted in 81 tapir encounters. Most encounters took place from 20:00-21:00 h (47%), which coincides with the main peak of activity estimated by radio-telemetry. Nocturnal line-transect sampling also provided some interesting information about the effect of moonlight intensity on tapir activity. Tapirs in Morro do Diabo were considerably less active during the brighter phases of the moon. Previous studies suggested that a lower level of animal activity during moonlit nights is a result of a higher predation risk (Leaver 2004; Meyer *et al.* 2004; Griffin *et al.* 2005; Lang *et al.* 2006). Regardless, this result could be biased by the fact that line-transect sampling in Morro do Diabo was carried out in dirt roads, where tapirs would be more vulnerable to predators such as jaguars and pumas during moonlit nights. Coelho *et al.* (2008) used camera-traps to evaluate the possible effects of moonlight on the frequency of use of natural licks by lowland tapirs in the Brazilian Pantanal. A similar frequency of use of licks by tapirs was recorded across all phases of the moon, and neither lunar phobia nor lunar philia were observed (Coelho *et al.* 2008). A camera-trap study carried out in Los Nevados National Park, Colombia, resulted in higher mountain tapir night time activity along trails and at a natural lick during the full moon (Lizcano & Cavelier 2000b).

Knowledge of tapir activity patterns is critical for understanding basic aspects of tapir biology and ecology. This information can be used to evaluate, select and adapt field methodologies while designing future research efforts. Given the predominant levels of activity occurring during crepuscular and nocturnal times, future studies focused on tapir species should concentrate research efforts during those periods. As pointed out by Wallace *et al.* (2002) and as evidenced by this study in Morro do Diabo, diurnal line-transect sampling may not be the most appropriate method to study primarily nocturnal animals such as tapirs, for which nocturnal censuses would be a better choice of method. Likewise, radio-telemetry studies on tapirs should concentrate data collection during times when tapirs are most active so as to increase the chances to obtain locations that will provide a good representation of tapir ranging behaviour. In addition, capture efforts for the placement of radio-collars should be performed in crepuscular and nocturnal periods. The information on tapir activity patterns obtained in Morro do Diabo has been already useful for the design of the Lowland Tapir Research and Conservation Programme established in the Brazilian Pantanal in 2008. In the Pantanal, I am using GPS telemetry to monitor tapirs and I have programmed the GPS collars to obtain at least 80% of the locations from 19:00-07:00 h.

5.4.2.2 Patterns of Tapir Habitat Use in Relation to Activity

Overall, tapirs in Morro do Diabo spent most of their active and inactive time in habitat types where they could have access to permanent water sources throughout the year. The same pattern was observed when running separate analyses for dry and wet seasons. These results corroborated the previous finding of this study that riparian habitats were strongly selected by tapirs and highly used in their main core areas. As a result, this provides evidence that tapirs in Morro do Diabo performed most of their foraging and resting activities in these habitats. Riparian habitats appeared to be particularly important for foraging activities, given that in most cases tapirs spent from 50-70% of their active time in these forests. On the other hand, tapirs spent very little of their active and inactive time in areas of agricultural and pastoral land, secondary forests, and temporary lakes. Therefore, tapirs did not seem to forage or rest in these habitat types, but only passed through them while travelling in between different patches of tall mature forest and riparian forests.

5.4.3 Spatial and Temporal Interactions between Lowland Tapirs and the Landscape and Implications for Population Viability

The semi-deciduous forests of Morro do Diabo are extremely heterogeneous, consisting of a complex mosaic of different habitat types in various states of conservation. In semi-deciduous forests, primary production of food resources is overall considerably lower and more unpredictable when compared to moister forests (Cullen *et al.* 2001a). In addition, the availability of water in these forests is very low (Cullen *et al.* 2001a). Most importantly, the habitat heterogeneity found in Morro do Diabo leads to different fruiting periods for different plant species found in different habitat types (Durigan & Franco 2006). Lowland tapirs are frugivores, and feed accordingly to the availability and abundance of fruit resources (Bodmer 1990a; Salas 1996). Thus, the spatial and temporal interactions between tapirs and the habitats available to them in Morro do Diabo were most likely determined by habitat heterogeneity. Tapirs included different types of habitat within their large home ranges so that they could encompass all the resources required to fulfil their energetic needs. Indeed, optimal foraging theory assumes that animals have complete knowledge of the spatial-temporal distribution of resources within their home ranges, allowing predictions of the resource depletion level at which an animal should leave each food patch (Stephens & Krebs

1986). Furthermore, large animals likely have a greater perceptual range (Zollner 2000), thereby influencing their ability to detect suitable habitat and perceive landscape structure and interrelatedness (Wiens 1996).

Tapirs in Morro do Diabo showed strong levels of selection for some of the available habitat types, particularly riparian forests. The concept of habitat selection precludes that an animal selects certain types of habitat in an attempt to maximise its survival, reproductive success, and the net rate of energy intake (MacArthur & Pianka 1966; Johnson 1980; Abrams 2000; Delibes *et al.* 2001). If this is deemed to be true, than species should survive and reproduce better (*i.e.* their fitness should be higher) in habitats that they tend to prefer (Rosenzweig & Abramsky 1986). Therefore, the strong selection tapirs have shown for riparian habitats clearly demonstrates the relative importance of these habitats in terms of tapir fitness when compared to other habitat types in Morro do Diabo. Tapirs in Morro do Diabo use riparian habitats for their main activities, particularly foraging, and therefore need them in order to survive, reproduce, and persist over the long-term.

Patterns of tapir habitat use and habitat selection observed in the 370 km^2 of forest of Morro do Diabo seemed to be different from results obtained in areas of contiguous moist forest, which are usually more homogeneous in terms of habitat types, and have higher primary production of food resources and more water. Tobler (2008) studied lowland tapirs in Los Amigos Research Station (1,400 km^2) in the Peruvian Amazon, and observed that habitat use varied with the availability of habitat types within the home ranges of the animals. However, given that most individuals had their home ranges exclusively in either one or two habitat types, they did not seem to select among habitats, the only exception being patches of *Mauritia flexuosa* palm swamp which were infrequently visited by some of the radio-collared tapirs (Tobler 2008).

Although tapirs in Morro do Diabo appeared to benefit from the existence of habitat types that fulfilled their nutritional requirements, the situation in the smaller forest fragments of the Pontal do Paranapanema Region might be different. Morro do Diabo provides for the large spatial requirements of tapirs. The forest fragments, on the other hand, are very small and extremely degraded. The impact of rural communities living in the vicinities of these small forest fragments, including erosion of forest edges by fires and cattle grazing, spread of aggressive weeds, and use of pesticides, have seriously modified forest structure and reduced habitat quality and carrying capacity for a number of species (Cullen 1997). The Morro do Diabo Management Plan describes the vegetation in most of the forest fragments surrounding Morro do Diabo as secondary forests in early stages of regeneration (Faria & Pires 2006). The plan states that most of these forests have been affected by several fire events over the last

40 years and are, therefore, mostly composed by tree species of early stages of regeneration, grasses and lianas.

The small forest fragments have very low diversity and availability of fruit, which is a serious limiting factor for the persistence of frugivore species such as tapirs. Tófoli (2006) analysed the impact of fragmentation of the Atlantic Forests of the Pontal do Paranapanema Region on the diet of tapirs and observed that tapirs in Morro do Diabo consumed significantly higher percentages of fruit (37%) and lower percentages of fibrous material (63%) when compared with tapirs in the smaller forest fragments (17% fruits, 83% fibrous materials). Furthermore, estimates of fruit species richness in the diet of tapirs indicated considerably higher fruit diversity in Morro do Diabo than in the forest fragments (Tófoli 2006). Lastly, the small forest fragments in the Pontal do Paranapanema Region are even poorer than Morro do Diabo in terms of availability of water. Therefore, these areas cannot provide tapirs with the riparian habitats they prefer and need for their main activities. Thus, results from this study provide enough evidence to say that the carrying capacity of these very small, largely degraded, non-protected forest fragments in the Pontal do Paranapanema Region might be indeed much lower when compared to Morro do Diabo. In consequence, tapirs in these small areas might not be given the proper conditions to fulfil their habitat requirements.

Nevertheless, evidence gathered during this study has shown that tapirs in the Pontal do Paranapanema Region move through the fragmented landscape in between different patches of forest. This characterises a tapir metapopulation scenario. During these landscape wonderings, tapirs move through areas of pasture land or agricultural crops. In some areas, tapirs cross patches of forest regeneration, degraded forest corridors, and riparian forests and swamps along small rivers. The fact that tapirs can use these marginal non-natural habitat areas surrounding the forests where they live, most certainly helps them fulfil both their spatial and habitat requirements in the smaller forest fragments. At any rate, tapir populations in the Pontal do Paranapanema Region still need recourse to Morro do Diabo in order to persist and be viable over the long-term.

Chapters 3, 4, and 5 focused on an empirical approach to assess the long-term persistence of lowland tapir populations in the Atlantic Forest fragments of the Pontal do Paranapanema Region. The next chapter will apply some of these results as well as information on tapir reproductive and mortality rates on modelling the viability of the tapir sub-populations and metapopulation in the Pontal do Paranapanema Region. Population Viability Analysis (PVA) carried out through the use of computer simulations will be used to model risks of extinction, Minimum Viable Population (MVP), impact of threats, and effects of conservation strategies, ultimately evaluating the viability of these tapir populations in the next 100 years.

Chapter 6

Population Viability Analysis (PVA): Using a Modelling Tool to Assess the Viability of Tapir Populations in a Fragmented Landscape

Photo by Patrícia Medici

6.1 Introduction

Population Viability Analysis (PVA) provides a quantitative means for predicting the probability of extinction and viability of a population (Shaffer 1981; Gilpin & Soulé 1986; Beissinger & Westphal 1998). PVA examines threats to persistence and evaluates the probability of a population of a specified size declining or going extinct over a specified length of time (Boyce 1992; Beissinger & Westphal 1998; Groom & Pascual 1998; Clark *et al.* 2002). Extinction risk is the likelihood of a population or species going extinct under various natural conditions and scenarios of management (Akçakaya 2000). The PVA process explores the consequences of different assumptions on population dynamics, especially for small populations (Lindenmayer & Lacy 1995) and evaluates which of a suite of management or conservation strategies is likely to maximise the probability of a population persisting over the long-term (Lindenmayer & Possingham 1996).

Simple empirical, analytical methods have yielded qualitative insights into population viability questions (Dennis *et al.* 1991). However, population growth is generally nonlinear, with nonlinear dynamics making most stochastic models intractable for analysis (Ludwig 1996). Catastrophes and their distribution pose even more difficult statistical problems (Ludwig 1996). Thus, analytical methods are generally inadequate to compute these probabilities. Consequently, Population Viability Analysis (PVA) is usually carried out through computer simulation models. Computer modelling is a valuable and versatile tool for analysing complex and interacting factors that influence population persistence, including natural and anthropogenic causes. These models incorporate the interacting deterministic and stochastic factors threatening animal populations and simulate the future of the species based on parameters on the ecology and demography of these populations (Burgman *et al.* 1993; Lacy 2000; Akçakaya 2000).

PVA works by using life-history or population growth-rate data to parameterise a population model that is then used to project population dynamics (Ludwig 1999). Under almost any set of circumstances, wildlife populations fluctuate in size over time. These fluctuations result from random (stochastic) variation acting on a set of processes - most notably birth, offspring sex ratio, dispersal, and death - that, acting together, determine the dynamics of population change. Numbers of individuals comprising a given population are determined largely by specified rates of reproduction, survival, and dispersal in addition to the ecological limitations of habitat carrying capacity. Variation in these rates is influenced by processes both intrinsic (demographic stochasticity, genetic drift and/or inbreeding depression, deviations in age or social structure) and extrinsic (environmental variation and catastrophic events) to the population (Shaffer 1981; Soulé 1987).

The primary use of PVA is to estimate the probability of extinction of a population, the mean time to extinction, or other measures of population performance such as growth rate, stability, or genetic diversity (Lacy 2000). The definitions and criteria for viability and extinction are set as arbitrary targets, such as a 95% probability of a population persisting for 100 years (Boyce 1992). A comparison of such measures of population viability for a set of different scenarios then allows comparison of which threats are most important. In addition, sensitivity analysis can be used to determine the primary demographic determinants of population growth (Wisdom & Mills 1997), and management alternatives can be compared to determine the most effective conservation strategies (Hamilton & Moller 1995).

A number of scientists have discussed the limitations of PVA (Beissinger & Westphal 1998; Coulson *et al.* 2001). However, the problem with PVA does not seem to be the model itself, but obtaining the data to drive it (Ruggiero *et al.* 1994). In a comprehensive study of the predictive capability of PVA modelling packages, Brook *et al.* (2000) demonstrated that, when adequately parameterised with reliable field data on the species or population of concern, PVA methods can provide a consistent technique for demographic population projection. Despite criticism, the use of PVA continues to grow and has become a valuable tool in the arsenal of conservation biologists (Beissinger & McCullough 2002). For example, PVA has become one of the primary tools for classification of threatened and endangered species by national wildlife management agencies and the International Union for Conservation of Nature (IUCN). PVA is a powerful method for classification because it provides objective, quantitative criteria on which decisions about risks of extinction can be made (Mace & Lande 1991). Furthermore, PVA is becoming increasingly important for both the formulation and implementation of conservation policy and legislation (Lindenmayer *et al.* 1993; Possingham *et al.* 1993).

In this Chapter, I focused on modelling the viability of tapir populations in the fragmented landscape of the Pontal do Paranapanema Region through the use of Population Viability Analysis (PVA). I used VORTEX software. First, I developed a robust VORTEX baseline model reflecting the biological potential of tapirs in Morro do Diabo, and carried out sensitivity analysis to evaluate the effect of selected reproductive and mortality parameters on the stochastic growth rate of this population. Second, I carried out an analysis of the Minimum Viable Population (MVP) for tapirs in Morro do Diabo. Third, I used the baseline model to evaluate the impact of potential catastrophes such as fire, and threats such as road-kill and infectious disease, analysing how these factors affect the probability of long-term persistence and viability of tapirs in Morro do Diabo. Lastly, I created a metapopulation scenario including Morro do Diabo and surrounding forest fragments in the Pontal do Paranapanema Region and analysed the probability of extinction of the different populations and of the metapopulation as a whole. As an example of conservation strategy, I modelled the establishment of corridors between Morro do Diabo and surrounding forest fragments, and analysed the impact this measure would have on the long-term viability of the lowland tapir populations in the region.

6.2 Methods

6.2.1 VORTEX Simulation Model

The modelling of the viability of the lowland tapir populations in the Atlantic Forests of the Pontal do Paranapanema Region, São Paulo, Brazil, was carried out through the use of VORTEX 9.94 software (Lacy 1993). VORTEX is a long-standing Population Viability Analysis (PVA) computer package that employs a Monte Carlo simulation of the impact of deterministic forces as well as demographic, environmental, and genetic stochastic events on wildlife population dynamics (Lacy 1993; Lacy 2000). It provides a platform to model many of the extinction vortices that can threaten persistence of small populations (hence, its name). VORTEX has been widely used to model the dynamics of wildlife populations (Miller & Lacy 2005).

VORTEX models population dynamics as discrete, sequential events that occur according to probabilities that are random variables following user-specified distributions. VORTEX is an individual-based model, which is mostly appropriate for analysing extinction dynamics in small populations (Lacy 2000). The software begins by creating individuals to form the starting population and stepping through life cycle events (*e.g.* births, deaths, dispersal, removals, supplementations) and catastrophic events, typically on an annual basis. Outcomes such as breeding success, litter size, sex at birth, and survival are determined based upon designated probabilities. As a result, each one of the iterations of the model generates distribution of fates that each individual, and consequently the population as a whole, might experience and gives a different result. By running the model hundreds of times, it is possible to examine the most probable outcome and the range of possibilities.

VORTEX is mostly used to simulate population trends, and evaluate current and future risk of population decline or extinction under alternative management scenarios (Lacy 2000; Miller & Lacy 2003). VORTEX is not intended to give absolute answers, since it is stochastically projecting the interactions of the several parameters used as input to the model and because of the random processes involved in nature. Interpretation of the output depends upon the knowledge of the biology of the species one is working with, the environmental conditions affecting the species, and possible future changes in these conditions. In essence, VORTEX provides a neutral platform upon which the user can examine the current status of a given species and determine which factors, if changed or manipulated, may have the greatest effect on causing or preventing extinction.

6.2.2 VORTEX Input Parameters: Baseline Model

A lowland tapir VORTEX baseline model was developed reflecting the biological potential of the species in Morro do Diabo. This baseline model was based on three main sources of data and information:

1) Data from this 12-year lowland tapir study in Morro do Diabo State Park.
2) Field and captivity data generated and/or compiled during previous Population and Habitat Viability Assessment (PHVA) Workshops held by the IUCN/SSC Tapir Specialist Group (TSG) and the IUCN/SSC Conservation Breeding Specialist Group (CBSG) for the four species of tapirs: Malayan Tapir PHVA Workshop, Malaysia, 2003 (Medici *et al.* 2003); Mountain Tapir PHVA Workshop, Colombia, 2004 (Lizcano *et al.* 2005); Baird's Tapir PHVA Workshop, Belize, 2005 (Medici *et al.* 2006); and Lowland Tapir PHVA Workshop, Brazil, 2007 (Medici *et al.* 2007a).
3) Published literature and personal observations on lowland tapir life table parameters, including information coming from both wild and captive studies.

6.2.2.1 Scenario Settings

- **Duration of Simulation:** The lowland tapir population in Morro do Diabo was modelled for 100 years, so that long-term population trends could be observed and evaluated. The generation length of lowland tapirs is estimated to be 11 years, considering age of sexual maturity at 3 years and longevity of ~25 years (IUCN 2008a). Therefore, a 100-year simulation covers ~9 generations. One hundred years is far enough into the future so as to decrease the chances of omitting a yet unknown event, but also not too short to fail to observe a slowly developing event.
- **Number of Iterations:** One thousand replicate simulations were run for each modelling scenario to provide adequate precision (Harris *et al.* 1987; Burgman *et al.* 1993).

6.2.2.2 Species Description

- **Definition of Extinction:** I defined extinction to mean the total removal of at least one sex. In other words, I was not looking at the decline of the population below some threshold size, otherwise known as quasi-extinction (Ginzburg *et al.* 1982).
- **Concordance of Environmental Variation (EV) between Reproductive Rates and Survival Rates:** No evidence of such concordance exists in tapir species. It is generally assumed that large, long-lived animals with long gestation periods show little

correlation between breeding and survival. Radio-tracked Baird's tapirs in Corcovado National Park, Costa Rica, continued to breed throughout the severe droughts of El Niño in 1997 and 1998 (C.R. Foerster, personal communication). Previous VORTEX modelling for all four species of tapirs did not include Concordance of Environmental Variation (EV) between reproductive rates and survival rates (Medici *et al.* 2003; Lizcano *et al.* 2005; Medici *et al.* 2006; Medici *et al.* 2007a).

- **Inbreeding Depression:** VORTEX has the ability to model the detrimental effects of inbreeding through reduced first-year survival of inbred individuals. Inbreeding is thought to have major effects on reproduction and survival, especially in small populations. As tapir populations continue to decline and become fragmented, genetic considerations are becoming very important. The impact of inbreeding was modelled as 3.14 Lethal Equivalents (LE), the median value estimated from an analysis of studbook data for 40 captive mammal populations (Ralls *et al.* 1988), with 50% of the effect of inbreeding ascribed to recessive lethal alleles.

6.2.2.3 Reproductive System and Rates

- **Breeding System:** Previous direct and indirect evidence from field studies on Baird's Tapirs in Corcovado National Park in Costa Rica indicate that tapirs are probably facultative polygymous (C.R. Foerster, personal communication). Previous VORTEX modelling for all four tapir species considered tapirs to be monogamous (Medici *et al.* 2003; Lizcano *et al.* 2005; Medici *et al.* 2006; Medici *et al.* 2007a). The reason behind this modelling decision relies on the fact that VORTEX is not spatially explicit and the selection of a polygymous system would suggest a panmictic scenario, which is less similar to what current data suggest than monogamy. Given that the sex ratio between males and females is equal and threats are generally not sex-specific, the choice of short-term monogamy or polygyny does not have an impact on population dynamics of lowland tapirs. For the purpose of this modelling, tapirs were categorised as "monogamous".
- **Age of First Reproduction:** VORTEX precisely defines reproduction as the time at which offspring are born and not the age of sexual maturity. The software uses the mean age rather than the earliest recorded age of offspring production. The earliest recorded conception of a female Malayan tapir at Saint Louis Zoo in the United States has been at 36 months (3 years), although females have bred as early as 31-32 months of age (Read 1986). Female Baird's tapirs in the wild reach sexual maturity from 2-3 years of age, and males at 3 (C.R. Foerster, personal communication). Eisenberg (1997) notes that a female lowland tapir does not become sexually mature until she is nearly 2 years of age under ideal conditions. According to Barongi (1993), captive lowland tapirs are usually sexually mature by 14-24 months and conceive at an average of 4 years of

age. At Madrid Zoo in Spain, a 27 months old female lowland tapir gave birth to a fully developed calf (Barongi 1993). At Rio de Janeiro Zoo in Brazil, a 30 months old female lowland tapir successfully gave birth to a healthy calf (G. Landau-Remy, personal communication). More recent results coming from the 2008 North-American Studbook for Lowland Tapirs show that female lowland tapirs reach their sexual maturity at 19 months of age (1.6 years) and first reproduce at 32 months (2.7 years) (D. Goff, AZA Lowland Tapir Studbook Keeper, personal communication). I assumed that natural situations impose a toll on growth and achieving sexual maturity, and thus assumed that both sexes are capable of siring their first offspring at age 4.

- **Maximum Age of Reproduction:** VORTEX initially assumes that animals can reproduce (at the normal rate) throughout their adult life. According to Eisenberg (1997), a female lowland tapir can remain reproductively active into her 10th year of life and beyond. According to Robinson & Redford (1986), the average age of last reproduction for wild lowland tapirs is 23 years. Results from the 2008 North-American Studbook for Lowland Tapirs indicate that the maximum age of reproduction for the species is 15 years for females and 19 years for males (D. Goff, AZA Lowland Tapir Studbook Keeper, personal communication). I set a maximum age of reproduction at 20 years for both males and females.

- **Maximum Number of Offspring per Year:** Data on gestation periods comes from captive tapir populations. The four species of tapirs have a gestation period of 13-14 months (390-407 days) (Barongi 1993). Older records from captive lowland tapirs have noted that this species have a gestation period from 335-439 days (von Richter 1966; Mallinson 1974). Inter-birth interval in captivity is close to 18 months (Barongi 1993). According to Eisenberg (1997), a female lowland tapir may conceive within a month after giving birth and under ideal circumstances a young can be born every 14 months in habitats exhibiting little seasonality in food availability. In seasonally dry habitats, the interval between births may be longer. For the purpose of this modelling I considered a maximum number of 1 offspring per year.

- **Maximum Litter Size:** Female tapirs rarely give birth to more than 1 young per litter (Barongi 1993). Only one twinning event was recorded in the 2008 North-American Studbook for Lowland Tapirs (D. Goff, AZA Lowland Tapir Studbook Keeper, personal communication). A female Malayan tapir held at the Malay Tapir Conservation Centre at the Sungai Dusun Wildlife Reserve in Malaysia gave birth to twin calves in May 2007. This was the first recorded twinning in Malayan tapirs (Z. Zainuddin & C. Traeholt, personal communication). However, these are rare events. For the purpose of the modelling, I considered a maximum litter size of 1 progeny.

- **Sex Ratio at Birth:** The 2008 North-American Studbook for Lowland Tapirs reports a sex ratio at birth of 3 males to 1 female (D. Goff, AZA Lowland Tapir Studbook Keeper, personal communication). However, there is no evidence to suggest a skewed sex ratio at birth in the wild. Among 35 different tapirs captured during this long-term study in Morro do Diabo, 20 were females and 15 were males, resulting in a sex ratio of 1.33 females to 1 male (57% females and 43% males). The sample size of 35 individuals represented ~30% of the tapir population in Morro do Diabo (~126 tapirs), and should therefore have yielded a fairly precise estimate of sex ratio for the population. Souza-Mazurek *et al.* (2000) monitored subsistence hunting among the Waimiri Atroari Indians in Central Amazon in Brazil and recorded a sex ratio of kills of 1.03 females to 1 male. Therefore, I assumed the sex ratio at birth to be 50% females and 50% males.

- **Female Breeding Success (Percentage of Adult Females Breeding):** As mentioned above, the inter-birth interval for captive tapirs is close to 18 months (Barongi 1993). A pair of lowland tapirs kept together at the National Zoo in the United States gave birth to 9 calves with an average inter-birth rate of 20 months (from 17-22 months) (Baker 1920). Other zoo evidences and field observations for wild Baird's tapirs in Corcovado National Park in Costa Rica indicate that females may become pregnant while lactating, which can reduce the interval to as few as 16 months (C.R. Foerster, personal communication). In addition, some females may lose their offspring during lactation, or due to stillbirths or neonatal deaths, and come into oestrus sooner afterward, therefore reducing the inter-birth interval. In a semi-captivity centre in Ecuador, the average interval between lowland tapir births was 19 months (A. Tapias, personal communication). For this modelling, I assumed that 60% of the females would be reproducing in a given year.

- **Environmental Variation in Breeding:** Annual environmental variation in female reproduction is modelled in VORTEX by specifying a standard deviation (SD) for the proportion of adult females that successfully produce offspring in a given year. No data are available for this parameter. Given their body size and reproductive rate, it is expected that tapirs show very little variation (Robinson & Eisenberg 1985). Assuming no variation in breeding may be less realistic than assuming a small variation. Thus, 10% of the initial rate, or 6%EV, was used in the simulation.

- **Density Dependent Reproduction:** Density dependent reproduction was not included in the baseline model for Morro do Diabo.

- **Mate Monopolisation:** In many species, some adult males may be socially restricted from breeding, despite being physiologically capable. Young males might be sexually mature but, because they are still dispersing or have not yet established their own territory, they might not be an effective part of the breeding pool. This can be modelled in VORTEX by specifying a portion of the total pool of adult males that may be considered "available" for breeding each year. Although there is a lack of field data about this parameter, it was considered that an average of 90% of the male tapirs in Morro do Diabo was reproducing each year.

6.2.2.4 Mortality Rates

There is virtually no data available on mortality rates for wild tapirs. However, some of the information gathered during this study in Morro do Diabo allowed me to attempt calculations of annual mortality of adult and sub-adult tapirs. A total of 25 tapirs (20 adults and 5 sub-adults) were radio-collared (Appendix II, for complete details about captured/radio-collared tapirs). Five of them died (3 adults and 2 sub-adults). Among the adults, two died of natural causes, and the third one was predated by jaguar. One of the adults that died of natural causes, an adult male, seemed to be very old and weak at the time of capture. I radio-collared the animal and recorded its death 25 days after the capture. Therefore, I did not include this animal on the calculations of mortality rates. Among the sub-adults (2 males), one was predated by puma and the other one by jaguar. By dividing the number of deaths (separately for adults and sub-adults) by the total number of months of radio-tracking, I calculated annual mortality rates of adult and sub-adult tapirs in Morro do Diabo. Monthly mortality of adult tapirs was 3/315=0.0095, which means that the monthly survival was 1-0.0095=0.9905 and that the annual survival was 0.9905^12=0.892. As a result, the estimated annual mortality for adult tapirs in Morro do Diabo was 10.8% (1-0.892=0.108). Similar calculations yielded a mortality rate of 29% for sub-adult tapirs in Morro do Diabo. When considering only the 14 tapirs radio-tracked from 8-36 months (Group 2), there were two records of adult mortality and no records of sub-adult mortality. Therefore, monthly mortality of adult tapirs was 2/293=0.0068, which means that the monthly survival was 1-0.0068=0.9932 and that the annual survival was 0.9932^12=0.9214. Annual mortality for adult tapirs in Morro do Diabo was 8% (1-0.9214=0.0786) according to the radio-tracking information from tapirs monitored in Morro do Diabo over the long-term. Similar calculations yielded a mortality rate of 0% for sub-adults.

For the purpose of this modelling, I set the mortality rate of adult tapirs in Morro do Diabo at 8%. Field studies on Baird's tapirs in Corcovado National Park, Costa Rica, demonstrated evidence of risk-prone behaviour in sub-adults from ages 3 to 5, which precludes a high mortality rate for this age class (C.R. Foerster, personal communication). However, I found the sub-adult mortality rate based on data from this study (29%) to be excessively high, probably due to small sample size of sub-adults. Therefore, I set the mortality rates of sub-adult tapirs (ages 1-2, 2-3, and 3-4) in Morro do Diabo at a more conservative 15%.

According to Eisenberg (1997), mortality in lowland tapirs may be heavy during the first year of life since predators (jaguar and puma) take younger animals. Additionally, zoo personnel attending the Lowland Tapir PHVA Workshop reported relatively high expected mortality of newborns. Therefore, I set the mortality rate for this age class at 10%. I assumed mortality rates to be equivalent between males and females. Standard deviations were calculated as 20% of the mortality rate, which seemed to provide a sensible interval. Mortality rates and standard deviations are presented in Table 6.1.

Table 6.1. Mortality rates and standard deviations estimated for different age classes of male and female tapirs in Morro do Diabo State Park, São Paulo, Brazil.

Age Class	Mortality Rate (%)	Standard Deviation (%)
From age 0 to 1	10	2
From age 1 to 2 - sub-adult	15	3
From age 2 to 3 - sub-adult	15	3
From age 3 to 4 - sub-adult	15	3
After age 4 - adult	8	1.6

6.2.2.5 Population Description

- **Number of Populations:** In the baseline model, only 1 population was considered (Morro do Diabo). Metapopulation dynamics was not explored at this stage.
- **Dispersal among Populations:** In the baseline model only 1 population was considered (Morro do Diabo), with no immigration or emigration of individuals.
- **Initial Population Size (N):** I used three values of initial tapir population size based on tapir densities estimated through three different methods: (i) Radio-telemetry: 126 tapirs; (ii) Footprint Identification Technique (FIT): 159 tapirs; and, (iii) Nocturnal line-transect sampling: 237 tapirs (Chapter 4, Table 4.6).
- **Carrying Capacity (K):** The carrying capacity was considered to be the same as the initial population size. In VORTEX, if the population size N exceeds K at the end of a particular time cycle, additional mortality is imposed across all age and sex classes in order to reduce the population back to this upper limit (Miller & Lacy 2005).
- **Catastrophe:** Reed *et al.* (2003) determined the frequency and severity of die-offs in 88 species of vertebrates. The authors noted that the frequency of severe die-offs in vertebrate populations is strongly related to the generation length of the organism and that the probability of a severe die-off for a particular population is ~14% per generation. The per year probability was calculated simply from the per generation probability by the following formula: P(Y)=P(G)/T. Where P(Y) is the probability of a catastrophe per year, P(G) is the probability of a catastrophe per generation (14%), and T is the generation length of the species (10 years for tapirs). P(Y)=0.014. Catastrophes

in Morro do Diabo could be fire or perhaps infectious disease. None of these catastrophes where thought to result in more than 10% decrease in tapir mortality or reproduction. For the purpose of this modelling, I included a catastrophe with a per year probability of 1.4% causing a 10% decrease in mortality and reproduction.

- **Harvest:** The model included harvest by road-kill. Currently, speed radars and educational sign posts have been placed on the highway crossing Morro do Diabo. As a result, only one tapir was killed on the highway over the last three years. For the purpose of this modelling, 1 male and 1 female were considered to be killed on the highway every 2 years.
- **Supplementation:** Supplementation from other unrelated populations, wild or captive, was not incorporated into the baseline model.

A compilation of all parameters used in the baseline model is presented in Table 6.2.

Table 6.2. Summary of parameter input values used in the VORTEX baseline model for the lowland tapir population in Morro do Diabo State Park, São Paulo, Brazil. (SD=standard deviation; LE=lethal equivalent).

Parameter	Baseline Value
Number of Populations	1
Initial Population Size (N)	**126** (radio-telemetry) **159** (FIT) **237** (line-transect)
Carrying Capacity (K)	Same as N
Inbreeding Depression	3.14 LE
% of the effect of inbreeding due to recessive lethal alleles	50
Breeding System	Monogamy
Age of First Reproduction (♀ / ♂)	4 years
Maximum Age of Reproduction	20 years
Annual % of Adult Females Reproducing (SD)	60% (6%)
Density Dependent Reproduction?	No
Maximum Litter Size	1
Overall Offspring Sex Ratio	50:50
% Adult Males in Breeding Pool	90
Mortality Rates:	
% Mortality from age 0-1 (SD)	10 (2)
% Mortality from age 1-2 (SD) - sub-adult	15 (3)
% Mortality from age 2-3 (SD) - sub-adult	15 (3)
% Mortality from age 3-4 (SD) - sub-adult	15 (3)
% Mortality from age above 4 (SD) - adult	8 (1.6)
Catastrophe*	YES
Harvest*	1♀ + 1 ♂ / 2 years
Supplementation	None

*These values were used in the baseline model as well as for the estimate of Minimum Viable Population (MVP)

6.2.3 Sensitivity Analysis

It is important to recognise that uncertainty regarding the biological parameters of a given population occurs at several levels especially for parameters that have never been measured in the population. Therefore, sensitivity testing is required to determine the extent to which uncertainty in input parameters results in uncertainty regarding the future fate of the population. This tool is used to uncover particularly sensitive parameters that, if changed, could significantly alter the results and conclusions derived from the model. If alternative plausible parameter values result in divergent predictions for the population, then it is important to resolve the uncertainty with better data to produce more confident results. Sensitivity of population dynamics to certain parameters indicates that those parameters describe factors that could be critical determinants of population viability. Additionally, sensitivity analysis evaluates the robustness of the baseline model to variations in selected parameter values. The more robust the model is to variations in a particular parameter, the less sensitive the model's results are to the input values of that parameter.

Sensitivity analysis was performed to evaluate the effect of reproductive and mortality parameters on the stochastic growth rate (r_{stoc}) of the lowland tapir population in Morro do Diabo. In each analysis, only one parameter was varied at a time, using the highest and lowest estimated values (Table 6.3). Results of sensitivity analysis were plotted against the (r_{stoc}) value observed for the baseline model. Catastrophe and harvest were not considered.

Table 6.3. Highest and lowest reproductive and mortality lowland tapir parameter values and standard deviations (SD) used for sensitivity analysis. (*Sub-adult mortality obtained from field data collected in Morro do Diabo State Park).

Parameter	Low	Baseline	Highest
% juvenile mortality (age 0-1)	5 (1)	10 (2)	20 (4)
% sub-adult mortality (age 1-4)	10 (2)	15 (3)	29 (5.8)*
% adult mortality (age above 4)	5 (1)	8 (2)	15 (3)
Age of first reproduction (♀)	3	4	5
Age of first reproduction (♂)	3	4	5
Annual % of adult females reproducing	50 (6)	60 (6)	65 (6)

6.2.4 Minimum Viable Population Analysis

The Minimum Viable Population (MVP) is an estimate of the minimum number of organisms of a particular species that constitutes a viable population over the long-term. More specifically, MVP is the smallest possible population size at which a biological population can exist without facing extinction from natural disasters or demographic, environmental, or genetic stochasticity (Shaffer 1981; Gilpin & Soulé 1986; Soulé 1987).

Lowland tapirs have a wide geographic distribution, across different biomes, where they face various types and levels of threats. It is thus almost impossible to establish a common definition of MVP for the species. In some areas, populations are small and fragmented, while in others, populations are large and contiguous. Therefore, an analysis of MVP depends on the objectives and measures used to characterise it. I carried out an analysis of the MVP for lowland tapirs in Morro do Diabo using two different measures:

- **Average probability that the population will go extinct ($P(E)_{100}$):** Extinction is defined in the model as no animals of one or both sexes remaining. $P(E)_{100}$ is determined by the proportion of the 1000 iterations within a given scenario that go extinct within 100 years. For the purpose of this modelling, I set a goal of $P(E)_{100}=0$.

- **The genetic diversity of the extant populations (GD):** It is expressed as a percent of the initial genetic diversity of the population that is maintained within 100 years. For the purpose of this modelling, I set a goal of maintaining 95% of genetic diversity after 100 years.

6.2.5 Modelling of Alternative Scenarios

The baseline model was used to analyse different scenarios and conservation challenges facing lowland tapirs in the Atlantic Forests of the Pontal do Paranapanema Region, including Morro do Diabo and surrounding forest fragments. I evaluated which factors, if changed or manipulated, may have the greatest effect on causing or preventing the extinction of lowland tapirs in the Pontal do Paranapanema Region. For some of these analyses, the baseline model excluded catastrophes and harvest as values for these threats were specifically tested.

The scenarios modelled as part of these analyses included:

(i) Impact of fire
(ii) Impact of road-kill
(iii) Impact of infectious disease
(iv) Metapopulation scenario
(v) Establishment of corridors

The measures used to evaluate results of different alternative scenarios were:

(i) Mean rate of stochastic population growth (r_{stoc})
(ii) Probability of extinction ($P(E)_{100}$)
(iii) Mean time to extinction (MeanTE)
(iv) Gene diversity of extant population (GD)
(v) Population size at the end of simulations (N-extant)

6.2.5.1 Impact of Fire

Fire was considered to be a potential catastrophe for the tapir population in Morro do Diabo and surrounding forest fragments. Catastrophes are singular environmental events that are outside of the bounds of normal environmental variation affecting animal survival and/or reproduction. Natural catastrophes include volcanic eruptions, tornadoes, fires, floods, droughts, and disease, among others. Catastrophes are modelled in VORTEX by assigning an annual probability of occurrence and a pair of severity factors describing their impact on survival (across all age and sex classes) and the proportion of females successfully breeding in a given year. These factors range from 0 (maximum or absolute effect) to 1 (no effect), and are imposed during the single year of the catastrophe, after which time the demographic rates rebound to their baseline values (Miller & Lacy 2005).

From 1963 to date, several forest fires have occurred in Morro do Diabo, most of them caused by fire management of pasture fields that accidentally entered Morro do Diabo (Faria & Pires 2006). The two major fire events occurred in 1968 and 1989, destroying 8 km^2 and 1.6 km^2 of forest respectively. For the purpose of modelling the impact of fire on the tapir population in Morro do Diabo, I modelled the occurrence of relevant fire events starting with a frequency of 1 event every 20 years (5%) and gradually increasing the frequency up to 1 event per year (100%). A relevant fire event was considered to destroy double the area destroyed by the major fire occurred in Morro do Diabo in 1968 (16 km^2), an area which according to tapir densities provided in Chapter 4 would host ~6 tapirs or roughly 5% of the resident tapir population when considering a population size of 126 individuals. Therefore, fire was modelled as a catastrophe that kills 5% of the tapirs in the population each time it occurs, but it does not affect reproduction.

6.2.5.2 Impact of Road-Kill

One of the main threats to lowland tapirs and many other animal species in Morro do Diabo is the highway that crosses the protected area (*SP-613 - Rodovia Estadual Arlindo Bétio*) (Figure 6.1.1). The Forestry Institute of São Paulo State, the governmental agency responsible for the administration of Morro do Diabo, and researchers from IPÊ - Instituto de Pesquisas Ecológicas have monitored the annual rates of road-kill on the highway for over a decade. From 1996 to 2006, an average of 6 tapirs were hit by cars and killed on the highway every year (Figure 6.1.2). In 1998 alone, 8 tapirs were killed. Most of the tapirs killed on the road were adult individuals capable of breeding. Since 2007, the Forestry Institute has taken several effective measures to reduce wildlife road-kill in Morro do Diabo. Speed radars and educational sign posts were placed on the highway and road-kill was drastically reduced. Over the last 3 years (2007-2009), only 1 tapir was killed on the SP-613 (A.S. Pires, Director of

Morro do Diabo State Park, personal communication). For the purpose of modelling the potential impact of this highway on the tapir population in Morro do Diabo, I used the Harvest mode of VORTEX, considering that 3 adult males and 3 adult females are killed every year.

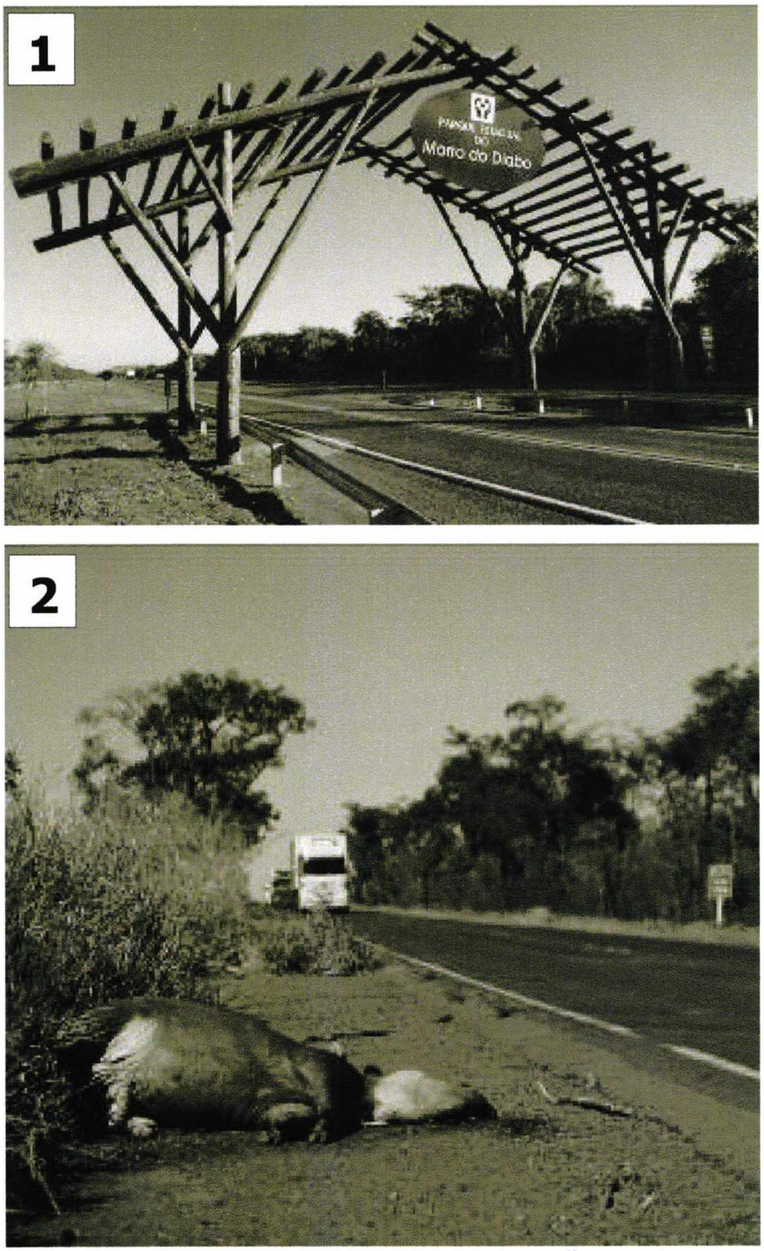


Figure 6.1. 1- Highway crossing Morro do Diabo State Park, São Paulo, Brazil; 2- Tapir road-kill. Photos by Patrícia Medici and Joares May.

6.2.5.3 Impact of Infectious Disease

This long-term study in Morro do Diabo has evaluated the prevalence of infectious diseases on the lowland tapir population. Blood samples collected from 32 of the tapirs captured were tested for 12 different infectious diseases relevant to tapirs and domestic livestock (horses, cattle, and swine) in the Pontal do Paranapanema Region including: <u>Viral Diseases</u>: Bluetongue, Infectious Bovine Rhinotracheitis, Foot and Mouth Disease, Equine Encephalitis (EEE-Eastern Equine Encephalitis & WEE-Western Equine Encephalitis), Bovine Viral Diarrhoea

(BVD), Bovine Viral Leucosis, New Jersey Vesicular Stomatitis, Aujeszky's Disease, Swine Parvovirus, and Equine Infectious Anaemia; Bacterial Diseases: *Brucella* spp and *Leptospira* spp. Positive titles were found for four diseases: Bluetongue (N=5), Infectious Bovine Rhinotracheitis (N=1), Equine Encephalitis (N=6 for both EEE and WEE), and *Leptospira* spp (N=8; sorovar *pomona* N=6; sorovar *Autumnalis* N=1; and sorovar *Hebdomadis* N=1). These results show that tapirs in Morro do Diabo have been exposed to diseases, especially Leptospirosis, which presented the highest prevalence of the study (25% of the tapirs).

Infectious disease can be modelled in VORTEX as a catastrophe that decreases survival and/or fertility of the individuals during the year(s) in which it occurs in the population. Once the disease has completed its cycle, the survival and/or fertility rates return to normal values and the population, if large enough and in the absence of other threats, can probably recover without further consequences. Thus, modelling an epidemic in VORTEX is not different from modelling the effects of a fire. An epidemic disease, however, once present will probably last in the population and in the environment for several generations. In addition, such pathogens usually do not kill their hosts, but often just reduce fertility and the lifetime of the carrier individuals, resulting in a reduction in the stochastic growth rate of the population. Nonetheless, the long-term results of this reduction are still unknown.

Using the baseline model, I modelled a closed lowland tapir population, in which all the individuals are already infected since the start with the bacteria that causes Leptospirosis (*Leptospira* spp). Judging from the effects of the bacteria on horses (domestic animals related to tapirs) and other wildlife species, veterinarians suggest that the presence of the disease can potentially cause a 1% increase in the mortality rate of all age classes, and a 5% decrease in the percentage of females breeding (P.R. Mangini, personal communication).

6.2.5.4 Metapopulation Scenario

There is a multitude of Atlantic Forest fragments of different sizes and levels of habitat disturbance throughout the Pontal do Paranapanema Region. Ditt (2002) surveyed all forest patches larger than 4 km^2 in the region (13 fragments). Lowland tapir presence was confirmed in seven of them, while no tapir evidence was found in the other six. During this study, 12 tapir dispersal routes between Morro do Diabo and surrounding forest fragments, as well as between the fragments amongst themselves were identified (Figure 6.2). The average distance between forest fragments was 4,150 m (varied from 1,318-8,950 m).

For the purpose of modelling the tapir metapopulation for the entire Pontal do Paranapanema Region, I included 8 different sub-populations: Morro do Diabo and the 7 forest fragments where tapirs were known to be present. I tested two different rates of tapir dispersal among forest patches as 1% or 0.5%. Additionally, I tested the impact of rate of tapir mortality during dispersal (10% or 0% mortality). Dispersing tapirs where individuals of both sexes from 2-4 years of age (sub-adults). Maximum and minimum population sizes were established using results of tapir densities provided in Chapter 4. In all the models, the carrying capacity (K) was equal to the initial population size. Nevertheless, I also tested what would happen if the carrying capacity of each of the forest fragments was much higher (K=100).

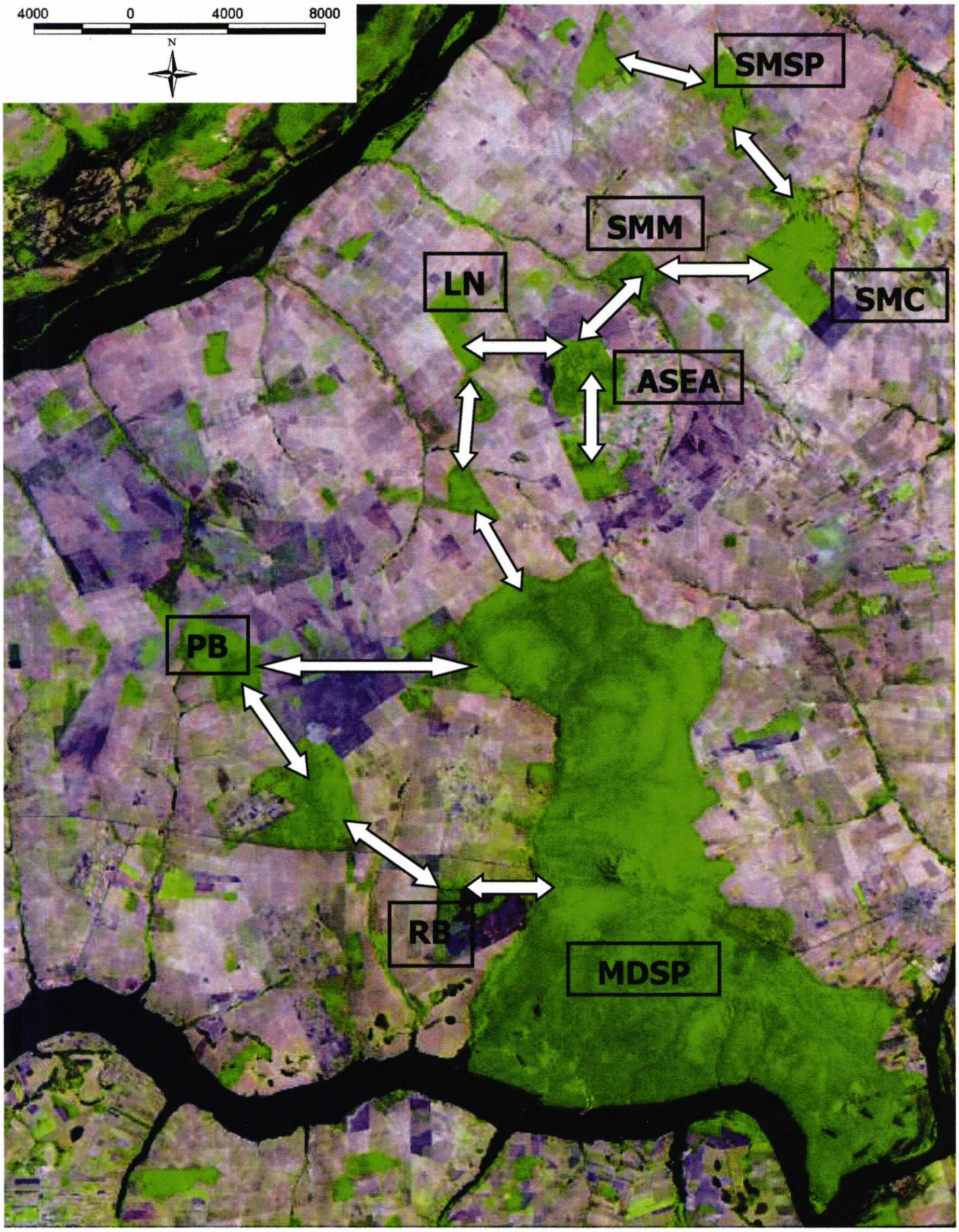


Figure 6.2. Potential routes of tapir dispersal between Morro do Diabo State Park (MDSP) and seven surrounding forest fragments where the presence of tapirs was confirmed (Ditt 2002) in the Pontal do Paranapanema Region, São Paulo, Brazil. (SMC: Santa Maria/Cachoeirinha; PB: Ponte Branca; ASEA: Água Sumida/Estrela da Alcídia; LN; Lua Nova/Santa Tereza da Água Sumida; SMM: Santa Maria dos Micos; SMSP: Santa Mônica/São Paulo; RB: Ribeirão Bonito). Figures 2.5 and 2.6 (Chapter 2) provide further reference on the location of Morro do Diabo State Park. Note: SMC, ASEA, and PB are part of the Black-Lion-Tamarin Ecological Station.

6.2.5.5 Establishment of Corridors

I modelled the establishment of corridors between Morro do Diabo and surrounding forest fragments, and analysed the impact the increase in landscape connectivity would have on the viability of the lowland tapir populations. The Landscape Restoration Programme of IPÊ - Instituto de Pesquisas Ecológicas has been working on the design and establishment of agro-forestry corridors and stepping-stones in the Pontal do Paranapanema Region for the past 14 years. A map of potential locations for the placement of recommended wildlife corridors has been designed (Figure 6.3).

The establishment of corridors would benefit the tapir populations of the Pontal do Paranapanema Region if they linked the different forest fragments together, and rates of tapir mortality were not increased when using corridors. For the purpose of modelling this scenario in VORTEX, the initial population size and carrying capacity were increased from 126 to 147 (radio-telemetry density estimate) or from 237 to 277 (line-transect sampling density estimate) (Table 6.4). I also tested what would happen if I included in this analysis the 6 forest fragments where tapirs were absent (Ditt 2002), increasing the initial population size and carrying capacity from 126 to 163 (radio-telemetry density estimate) or from 237 to 307 (line-transect sampling density estimate) (Table 6.4).

Figure 6.3. Potential locations for the establishment of agro-forestry corridors connecting Morro do Diabo State Park to surrounding forest fragments in the Pontal do Paranapanema Region, São Paulo, Brazil. Map designed by IPÊ - Instituto de Pesquisas Ecológicas. Figures 2.5 and 2.6 (Chapter 2) provide further reference on the location of Morro do Diabo State Park.

Table 6.4. Estimates of lowland tapir population sizes in Morro do Diabo State Park and seven forest fragments where the presence of tapirs was confirmed (Ditt 2002) (A), and potential carrying capacity of six forest fragments where tapirs were absent (B). Estimates of tapir population size were based on densities obtained by radio-telemetry, nocturnal line-transect sampling, and Footprint Identification Technique. (*Potential carrying capacity of fragments where tapirs were absent; **Potential total population size including forest fragments where tapirs were absent).

MDSP & Forest Fragments	Area (km^2)	Population Size (number of individuals) **Radio-Telemetry** 0.34 tapirs km^{-2}	**FIT** 0.43 tapirs km^{-2}	**Line-Transect** 0.64 tapirs km^{-2}
Morro do Diabo State Park (MDSP)	**370.0**	**126**	**159**	**237**
Santa Maria / Cachoeirinha (SMC)	18.3	6	8	12
Ponte Branca (PB)	13.0	4	6	8
Água Sumida / Estrela da Alcídia (ASEA)	12.1	4	5	8
Lua Nova / Santa Tereza da Água Sumida (LN)	5.4	2	2	3
Santa Maria Micos (SMM)	5.1	2	2	3
Santa Mônica / São Paulo (SMSP)	4.9	2	2	3
Ribeirão Bonito (RB)	4.2	2	2	3
Total population size in fragments where tapirs are present (A)		**22**	**27**	**40**
Tucano (TU)	18.0	0 (6*)	0 (8*)	0 (12*)
Santa Rita (SR)	8.7	0 (3*)	0 (4*)	0 (5*)
Água Sumida / Santa Maria (ASSM)	5.5	0 (3*)	0 (2*)	0 (4*)
6R (6R)	4.3	0 (1*)	0 (2*)	0 (3*)
Nova Pontal (NP)	4.3	0 (1*)	0 (2*)	0 (3*)
Água do Peão (AP)	4.2	0 (1*)	0 (2*)	0 (3*)
Carrying capacity in fragments where tapirs are absent (B)		**15**	**20**	**30**
Total Tapir Population (MDSP + fragments A) Potential Total Tapir Population (MDSP + A + B)		**148** (163**)	**186** (206**)	**277** (307**)

Note: SMC, PB, ASEA, and TU are the fragments that compose the Black-Lion-Tamarin Ecological Station.

6.3 Results

6.3.1 VORTEX Baseline Model

The VORTEX baseline model of the lowland tapir population in Morro do Diabo was based on the parameters previously described and reflected the biological potential of the species in Morro do Diabo. These parameters were based on the biology of this population in the absence of stochastic fluctuations (both demographic and environmental variation), inbreeding depression, limitation of mates, and immigration or emigration.

6.3.1.1 Deterministic Output

The demographic rates (reproduction and mortality) included in the baseline model were used to calculate deterministic characteristics of the model population. The baseline model resulted in a deterministic growth rate (r_{det}) of 0.047 (λ= 1.048). This represented a potential annual growth rate of almost 5%, which enables the population to grow when below carrying capacity. Generation time (the average age of reproduction) resulted in ~10 years for both males and females. Adult sex ratio of adult males to adult females was 1. Overall, these population characteristics were accepted as realistic for lowland tapirs and lend validity to this model as a reasonable representation of the lowland tapir population in Morro do Diabo.

6.3.1.2 Stochastic Baseline Results

Results from the baseline model projected that a population of 126 tapirs (Radio-telemetry Method 2 density estimate, 0.34 tapirs km^{-2}), in the complete absence of catastrophes and threats, is likely to persist over the next 100 years. The stochastic growth rate (r_{stoch}) of this population was 0.040, probability of extinction was zero, and the population size at the end of simulations at 100 years N-extant was 124 tapirs with 92% of genetic diversity remaining. When including catastrophe and harvest as described in the baseline model, the population still appears to be capable of persisting over the next 100 years. However, the stochastic growth rate (r_{stoch}) was reduced to 0.029, N-extant was 122 tapirs, and 92% of genetic diversity remaining.

6.3.2 Sensitivity Analysis

The results from the sensitivity analysis showed that the parameters sub-adult mortality and adult mortality have the strongest influence on the dynamics of lowland tapir populations (Figure 6.4). The age of first reproduction for female tapirs appeared to be a sensitive parameter as well.

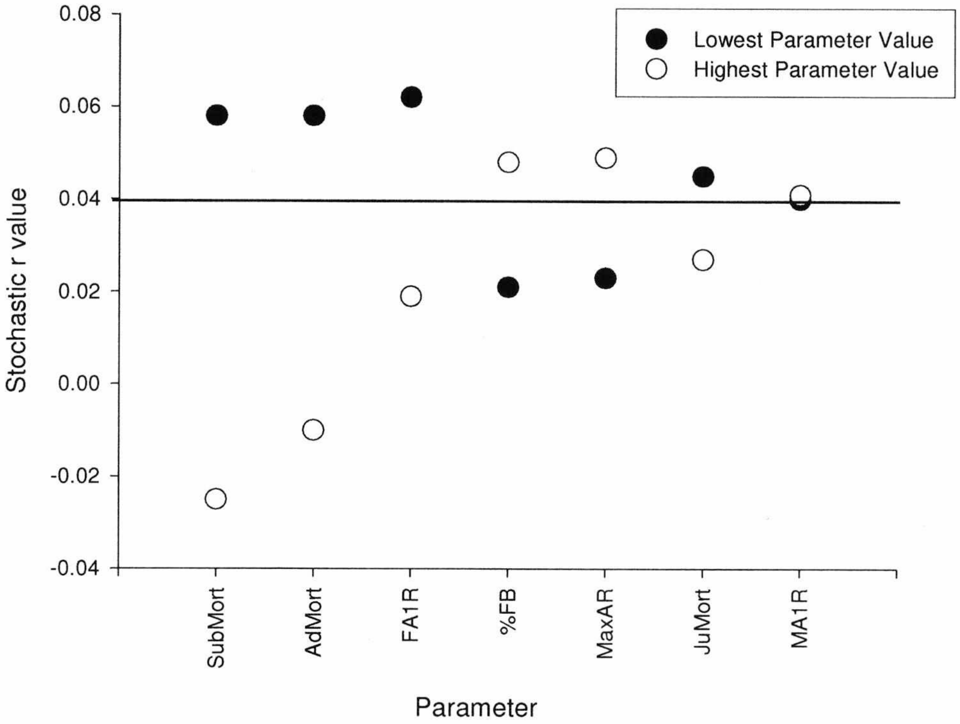


Figure 6.4. Results from sensitivity analysis. The line represents the value of stochastic population growth from the baseline model (SubMort: Sub-adult mortality; AdMort: Adult mortality; FA1R: Age of first reproduction for females; %FB: Annual percent of adult females breeding in the population; MaxAR: Maximum age of reproduction; JuMort: Juvenile mortality; MA1R: Age of first reproduction for males)

6.3.3 Minimum Viable Population (MVP)

MVP was previously defined as a population of tapirs with $P(E)_{100}=0$ and 95% of genetic diversity remaining after 100 years. According to the VORTEX model, ~200 individual tapirs would be necessary to maintain a viable population for the next 100 years (Table 6.5).

Table 6.5. Results of genetic diversity (GD, %), probability of extinction ($(P(E)_{100}$, in %), mean rate of stochastic population growth (r_{stoc}), and population size at the end of simulations (N-extant) obtained through the analysis of Minimum Viable Population (MVP) for lowland tapirs.

Population Size (N)	GD (%)	$P(E)_{100}$ (%)	r_{stoc}	N-extant
25	0	100	-0.063	0
50	77	67	-0.013	30
75	86	6	0.014	61
100	90	0	0.024	94
125	92	0	0.028	121
150	93	0	0.032	147
175	94	0	0.034	172
200	**95**	**0**	**0.035**	**197**
225	95	0	0.037	223
250	96	0	0.037	247
275	96	0	0.038	273
300	96	0	0.038	297

6.3.4 Modelling of Alternative Scenarios

6.3.4.1 Impact of Fire

As the frequency of fire events increased, the stochastic growth rate of the tapir population in Morro do Diabo dramatically decreased. In addition, as the size of the tapir population increased, the impact of fire events decreased (Figure 6.5).

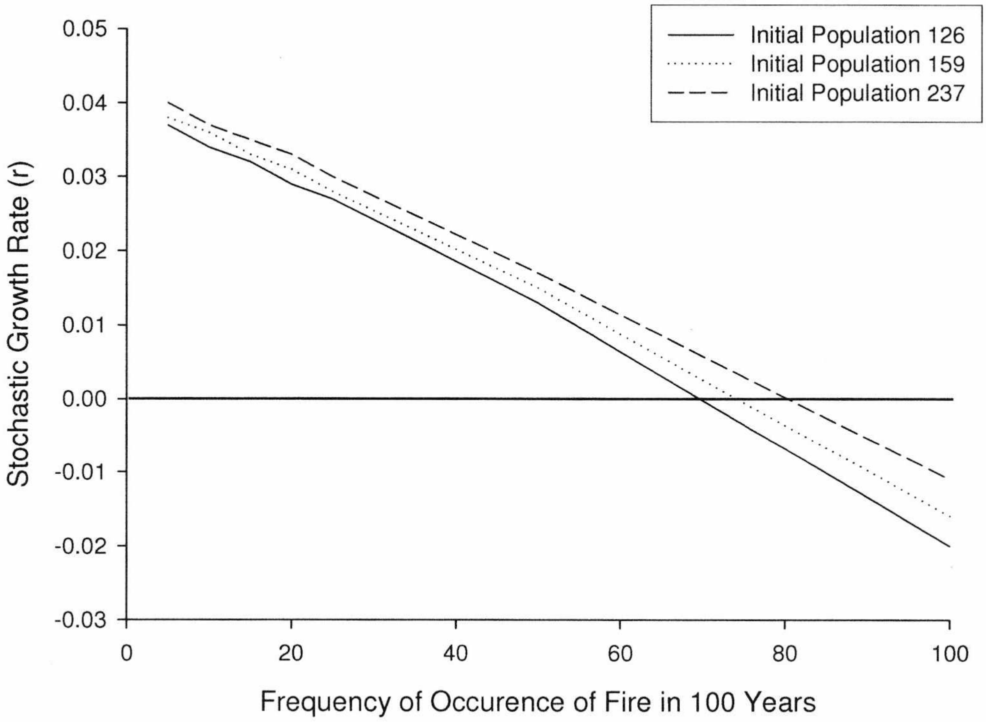


Figure 6.5. Impact of fire events on stochastic growth rate as the frequency of fires increases for populations of tapir with different initial population sizes (N=126; N=159; N=237).

6.3.4.2 Impact of Road-Kill

Removing 6 adult tapirs (3 females and 3 males) from the population every year due to road-kill had a major impact on the tapir population of Morro do Diabo. A tapir population of 126 individuals (radio-telemetry estimate) resulted in a 100% probability of extinction in 100 years. Nevertheless, the higher the initial population size, the lower the probability of extinction (Table 6.6). Road-kill also reduced the genetic diversity of the population.

Table 6.6. Results of mean rate of stochastic population growth (r_{stoc}), probability of extinction ($P(E)_{100}$, %), mean time to extinction in years (MeanTE, years), genetic diversity of extant population (GD, %), and population size at the end of simulations (N-extant) obtained through the analysis of the impact of road-kill on the lowland tapir population in Morro do Diabo State Park.

Population Size (N)	r_{stoc}	$P(E)_{100}$ (%)	**MeanTE** (years)	**GD** (%)	**N-extant**
126	-0.082	100	38	0	0
159	-0.043	88	61	91	85
237	0.013	3	78	95	215

6.3.4.3 Impact of Infectious Disease

A disease such as Leptospirosis can cause a 1% increase in the mortality rate of all tapir age classes, and a 5% decrease in percentage of females breeding in the population (P.R. Mangini, personal communication). When using an initial population size and carrying capacity of 126 individual tapirs, the impact of the disease caused a decrease of stochastic growth rate (r_{stoch}) from 0.040 to 0.019, which amounts to a decrease of almost 50%. When using an initial population size and carrying capacity of 237 tapirs, (r_{stoch}) decreased from 0.043 to 0.023. In both cases, the impact of the disease did not increase the probability of extinction of tapirs.

6.3.4.4 Metapopulation Scenario

Without dispersal from Morro do Diabo, all the tapir populations in the small forest fragments of the Pontal do Paranapanema Region will go extinct over the next 100 years. However, this dispersal of individuals from Morro do Diabo to the forest fragments had a major impact on the resident tapir population of Morro do Diabo. In the absence of dispersal, the tapir population growth in Morro do Diabo was almost 4%. For an initial population size of 126 tapirs in Morro do Diabo (radio-telemetry estimate), a 1% dispersal of tapirs aged from 2-4 years (sub-adults), decreased the growth rate in Morro do Diabo to almost 0% (Table 6.7). When decreasing the dispersal rate by half (0.5%), the tapir population in Morro do Diabo maintained a population growth rate of 2% (Table 6.7). When considering an initial population size of 237 tapirs (line-transect sampling estimate), a 1% dispersal of tapirs from Morro do

Diabo still reduced the growth rate in Morro do Diabo to ~1%, while a 0.5% dispersal rate maintained an almost 3% growth rate (Table 6.8). In VORTEX, if the initial population size exceeds the carrying capacity at the end of a particular time cycle, additional mortality is imposed across all age and sex classes in order to reduce the population back to this upper limit (Miller & Lacy 2005). Therefore, due to their small sizes, the forest fragments are acting as sink habitats for tapirs dispersing from Morro do Diabo and decreasing the stochastic growth rate of the tapir population in Morro do Diabo. The probability of survival of tapirs during dispersal did not impact the tapir population in Morro do Diabo as much as this loss of tapirs due to the low carrying capacity of the small fragments (Tables 6.7 and 6.8). Dispersal rate, rather than survival during dispersal or initial population size, was the parameter that had the most impact on the overall tapir metapopulation in the Pontal do Paranapanema Region.

If the forest fragments were larger and had a potential carrying capacity of 100 tapirs each, the stochastic growth rate of Morro do Diabo would be less impacted as fewer animals would die as a result of lack of habitat carrying capacity (Table 6.9). The forest fragments still acted as a sink for Morro do Diabo. However, the lower the tapir dispersal rates between Morro do Diabo and the forest fragments, the higher the stochastic growth rate of the tapir population in Morro do Diabo.

Table 6.7. Impact of probability of survival and dispersal rate on stochastic growth rate and probability of extinction (%) of the lowland tapir sub-populations and metapopulation in the Pontal do Paranapanema Region, São Paulo, Brazil (radio-telemetry estimate, N=126).

Sub-Populations & Metapopulation	**1% dispersal**				**0.5% dispersal**			
	90% survival		**100% survival**		**90% survival**		**100% survival**	
	r_{stoc}	$P(E)_{100}$	r_{stoc}	$P(E)_{100}$	r_{stoc}	$P(E)_{100}$	r_{stoc}	$P(E)_{100}$
MDSP	**0.002**	**1**	**0.003**	**0**	**0.022**	**0**	**0.022**	**0**
SMC	-0.010	98	-0.007	97	-0.008	100	-0.007	100
PB	0.166	22	0.182	20	0.110	27	0.120	24
ASEA	0.161	24	0.177	21	0.105	28	0.115	23
SMM	0.167	99	0.172	98	0.158	100	0.161	100
SMSP	0.158	100	0.159	100	0.152	100	0.152	10
RB	0.545	61	0.582	64	0.389	62	0.411	62
LN	0.151	100	0.154	100	0.151	100	0.149	100
METAPOPULATION	**0.028**	**0**	**0.031**	**0**	**0.032**	**0**	**0.034**	**0**

Table 6.8. Impact of probability of survival and dispersal rate on stochastic growth rate and probability of extinction (%) of the lowland tapir sub-populations and metapopulation in the Pontal do Paranapanema Region, São Paulo, Brazil (line-transect estimate, N=237).

Sub-Populations & Metapopulation	**1% dispersal**				**0.5% dispersal**			
	90% survival		**100% survival**		**90% survival**		**100% survival**	
	r_{stoc}	$P(E)_{100}$	r_{stoc}	$P(E)_{100}$	r_{stoc}	$P(E)_{100}$	r_{stoc}	$P(E)_{100}$
MDSP	**0.007**	**0**	**0.007**	**0**	**0.026**	**0**	**0.026**	**0**
SMC	-0.009	89	-0.007	87	-0.008	94	-0.007	92
PB	0.178	2	0.195	1	0.105	2	0.116	3
ASEA	0.191	3	0.212	2	0.114	4	0.126	3
SMM	0.056	95	0.059	92	0.042	98	0.048	98
SMSP	0.044	100	0.049	99	0.039	100	0.039	100
RB	0.701	35	0.756	34	0.460	35	0.492	35
LN	0.030	100	0.032	100	0.027	100	0.027	100
METAPOPULATION	**0.034**	**0**	**0.037**	**0**	**0.037**	**0**	**0.038**	**0**

Table 6.9. Impact of dispersal rate on stochastic growth rate of the lowland tapir sub-populations and metapopulation in the Pontal do Paranapanema Region, São Paulo, Brazil, considering a carrying capacity of 100 tapirs in each forest fragment, 90% of survival during dispersal (radio-telemetry estimate, N=126).

Sub-Populations & Metapopulation	r_{stoc}	
	1% dispersal	**0.5% dispersal**
MDSP	**0.024**	**0.032**
SMC	0.027	0.021
PB	0.051	0.051
ASEA	0.040	0.037
SMM	0.041	0.040
SMSP	0.047	0.036
RB	0.065	0.057
LN	0.044	0.030
METAPOPULATION	**0.034**	**0.036**

6.3.4.5 Establishment of Corridors

The establishment of corridors was modelled as an increase in landscape connectivity. The initial population size and carrying capacity were increased from 126 to 148 individuals (radio-telemetry estimate), and from 237 to 277 individuals (line-transect estimate) (Table 6.10). The increase from 126 to 148 tapirs did not result in an increase in stochastic growth rate, but presented an increase in percentage of genetic diversity maintained (Table 6.10). The increase from 237 to 277 tapirs resulted in a fairly small increase in stochastic growth rate (Table 6.10).

Similarly, when adding to the analysis the potential carrying capacity of the forest fragments where tapirs were absent - increase in the initial population size and carrying capacity from 126 to 163 (radio-telemetry estimate), or from 237 to 307 (line-transect estimate) (Table 6.4) - increases in tapir population's stochastic growth rate and genetic diversity were observed.

Table 6.10. Impact of the establishment of corridors on the stochastic growth rate (r_{stoc}), probability of extinction ($P(E)_{100}$), population size at the end of simulations (N-extant), and genetic diversity of extant population (GD) of the lowland tapir sub-populations in the Pontal do Paranapanema Region, São Paulo, Brazil (radio-telemetry estimate: MDSP - Morro do Diabo State Park=126 tapirs, Entire population=147 tapirs; line-transect estimate: MDSP=237 tapirs, Entire population=277 tapirs).

Population Size (N)	r_{stoc}	$P(E)_{100}$ (%)	**N-extant**	**GD** (%)
WITHOUT Corridors N=126 (MDSP)	0.040	0	124	92
WITH Corridors N=148 (Entire Population)	0.040	0	145	93
WITHOUT Corridors N=237 (MDSP)	0.043	0	235	96
WITH Corridors N=277 (Entire Population)	0.044	0	275	96

6.4 Discussion

6.4.1 Biological Potential of Tapirs in Morro do Diabo State Park

The resulting VORTEX baseline model projected the biological potential of the tapir population in Morro do Diabo. The resulting potential annual growth rate of almost 5% enables the population to grow when below carrying capacity. Nevertheless, this growth rate provided evidence that even in the absence of additional threats or stochastic events, the tapir population in Morro do Diabo will not grow very rapidly and, most importantly, will take a considerable amount of time to recover from any events that severely reduce their numbers.

Results from the baseline model projected that a tapir population of 126 tapirs is likely to persist in Morro do Diabo over the next 100 years, even when facing regular fire events and annual road-kill. However, while the probability of extinction was zero, only 93% of genetic diversity remained at the end of simulations at 100 years. The loss of genetic diversity was in part due to the relatively small population size and also because I modelled a closed population in which no immigration of unrelated animals occurred.

6.4.2 Sensitivity Analysis: Uncertainty in Input Parameters

The results from the sensitivity analysis showed that the parameters sub-adult mortality and adult mortality have the strongest influence on the dynamics of the lowland tapir population in Morro do Diabo. Tapirs are long-lived, late maturing species with slow reproductive rates and these species are typically characterised by high adult survival (Oli & Dobson 2003). This means that any threats impacting this parameter, such as hunting or road-kill of adults will have a major impact on the tapir population. The age of first reproduction for female tapirs appeared to be a sensitive parameter as well. This might be explained by the fact that a year of sub-adult mortality (the highest mortality rate of all age classes) is either added or subtracted along with the age of first reproduction for females. Therefore, this parameter actually shows the impact of sub-adult mortality. These results show that it would be extremely important to obtain more accurate values of tapir mortality rates in the wild. Obtaining more accurate values for these parameters would be critical to improve current VORTEX models for lowland tapirs. The more accurate the parameters used are, the more robust the model is. Nevertheless, as shown by this long-term lowland tapir study in Morro do Diabo, accurate estimates for these parameters in wild populations of tapirs are the most difficult to obtain.

6.4.3 Minimum Viable Population (MVP): Morro do Diabo State Park

One of the most important results of the PVA for the lowland tapir population in Morro do Diabo was the estimate of Minimum Viable Population (MVP). While population size is the major determinant of persistence in populations of a variety of animal species (Brown 1971; Jones & Diamond 1976; Toft & Schoener 1983; Diamond *et al.* 1987; Newmark 1987; Pimm *et al.* 1988; Richman *et al.* 1988; Soulé *et al.* 1988; Berger 1990; Kindvall & Ahlén 1992; Schoener & Spiller 1992; Foufopoulos & Ives 1999), controversy remains as to how large these populations need to be to ensure long-term persistence (Reed *et al.* 2003).

The analysis of tapir MVP for Morro do Diabo considered two very strict parameters including zero probability of extinction and 95% of genetic diversity remaining after 100 years. In particular, maintenance of genetic diversity should be seriously taken into consideration given that small populations may persist in the model, but suffer such loss of genetic diversity resulting in deleterious genes impacting the population over the long-term. According to the VORTEX model, ~200 individual tapirs would be required to maintain a viable tapir population in Morro do Diabo for the next 100 years. Thus, this modelling provided evidence that the estimated tapir population of 126 tapirs in Morro do Diabo is not large enough to be viable over the long-term. While it is likely to persist over the next 100 years, it is not large enough to maintain 95% of genetic diversity. Thus, conservation measures must be taken in order to promote maintenance of genetic diversity in Morro do Diabo.

6.4.4 Modelling of Scenarios: Threats, Metapopulation and Conservation Strategies

6.4.4.1 Impact of Threats: Fire

Fire was modelled as a catastrophe. The VORTEX modelling showed that as the frequency of fire events increased, the stochastic growth rate of the tapir population in Morro do Diabo decreased. Fortunately, the frequency of fires in Morro do Diabo is much lower nowadays since several effective measures have been taken to prevent forest fires in Morro do Diabo. Nevertheless, the modelling did illustrate that future fire events could potentially decrease the resilience of the tapir population in Morro do Diabo to other threats, ultimately compromising their long-term persistence. More importantly, the VORTEX model demonstrated that the smaller the tapir population, the higher the impact of fires. This provided evidence that in the smaller forest fragments of the Pontal do Paranapanema Region, where the initial population size of resident tapirs is considerably lower, the impact of fire could be potentially catastrophic.

In order to perfect the modelling of the impact of fires on tapirs, it would be necessary to estimate the number of tapirs killed, as well as the ability of tapirs to escape and walk away from burning zones. Silveira *et al.* (1999) evaluated the impact of two wildfires on the large mammal fauna in the *Cerrado* of Emas National Park, central Brazil. One of these fires, in 1994, was particularly large and burned 100% of Emas grasslands, and killed 13 giant anteaters, 2 giant armadillos, and 1 juvenile tapir. The authors noted that tapirs are most probably less vulnerable to fire because they can detect it and run from the flames more rapidly. Koproski (2005) studied the impact of fire on the community of mammals in the forests and floodplains of the Ilha Grande National Park in Mato Grosso do Sul State, Brazil, and from a helicopter observed a tapir walking away from a large forest fire.

6.4.4.2 Impact of Threats: Road-Kill

Among the most widespread forms of modification of natural landscapes during the past century has been the construction and maintenance of roads (Diamondback 1990; Bennett 1991; Noss & Cooperrider 1994). As conservation biologists seek to understand the forces that influence the viability of animal populations, it is critical that we understand the scope of the ecological effects of roads (Trombulak & Frissell 2000). Roads affect ecosystems in many different ways, one of these being the increased mortality of animals from collisions with vehicles. Road-kill can have a major effect on animal populations (Spellerberg 1998; Trombulak & Frissell 2000; Kerley *et al.* 2002).

From 1996 to 2006, an average of six tapirs were hit by cars and killed every year on the highway that crosses Morro do Diabo. To make matters worse, it is very probable that even more tapirs were killed on the road, given that some tapirs may have been removed for meat consumption. The VORTEX model showed that losing six adult tapirs to road-kill every year has a major impact on the resident tapir population of Morro do Diabo. This level of road-kill would lead the estimated tapir population of 126 tapirs to extinction in ~38 years. As demonstrated in the sensitivity analysis, adult mortality is a very sensitive parameter for tapirs and therefore road-kill greatly reduces the stochastic growth rate.

Fortunately, since 2007, the Forestry Institute of São Paulo State has taken several effective measures to reduce wildlife road-kill in the highway. Speed radars and educational sign posts were placed along the highway and tapir road-kill was drastically reduced. Over the last three years (2007-2009), only one tapir was killed on the highway. Nevertheless, road-kill is still considered a serious threat to tapirs in Morro do Diabo. In fact, road-kill is one of the major threats to lowland tapirs in other parts of the Atlantic Forest, as well as in the Cerrado and Pantanal biomes. In April 2009, I observed and photographed seven dead tapirs, all adults, killed in a section of less than 10 km of a highway that connects the western part of São Paulo

State to the Pantanal, through the Cerrado. The VORTEX modelling demonstrated very clearly the kind of impact mortality like this can impose on a population of tapirs.

6.4.4.3 Impact of Threats: Infectious Disease (Leptospirosis)

Disease is frequently mentioned as a serious threat to wildlife species (Fiorello *et al.* 2006). However disease risk has proven to be very complex and difficult to assess and quantify, there is growing recognition that disease issues can profoundly affect the viability of populations and consequently the success or failure of conservation programs. Most diseases impacting animal conservation are infectious in origin, although genetic and toxic diseases also influence population viability (Munson 2003). In herbivores in general, and in ungulates in particular, there are several known diseases affecting cattle and other domestic animals, such as horses and swine, which are problematic from the point of view of wildlife health (*e.g.* foot-and-mouth disease). Regarding tapir species, there is only one published study about the health of free-ranging Baird's tapirs in Corcovado National Park, Costa Rica (Hernández-Divers *et al.* 2005). Overall, there is very little information available to understand the potential individual and population effects of both epidemic and endemic diseases on tapirs.

In Morro do Diabo, tapirs were positive for four types of infectious disease. Leptospirosis presented the highest prevalence of the study (25% of 32 sampled tapirs). Leptospirosis is an acute, febrile and infectious disease, caused by a bacterium of the genus *Leptospira*. This disease is distributed worldwide and has a complex epidemiology. It affects both wildlife and domestic livestock. Rodents are the main hosts. Nava (2008) conducted an epidemiological survey of the domestic livestock in the Pontal do Paranapanema Region and observed that 33% of the horses in the region were positive for Leptospirosis. The fact that tapirs and horses are closely related and due to the high possibility of contact between the two species in the areas alongside the edges of Morro do Diabo could explain the high prevalence of this disease in this tapir population. However, five of the eight tapirs were positive for Leptospirosis were captured and had their home ranges in the centre of Morro do Diabo, far away from the borders, and where tapirs were unlikely to encounter livestock. This provided evidence that the Leptospirosis bacteria are indeed spread throughout Morro do Diabo and the entire tapir population might have been exposed. Furthermore, this provides evidence that disease can be more spread in wild tapir populations than previously thought.

Judging from the known effects of the Leptospirosis bacteria on horses and other wildlife species, this disease can potentially cause an increase in tapir mortality rates, as well as a decrease in the percentage of females breeding in the population (P.R. Mangini, personal communication). With this kind of impact, the estimated tapir population of 126 tapirs in Morro do Diabo showed a decrease in growth rate. A decrease in the stochastic growth rate means that the population will recover more slowly from other threats or events that decrease its population size. The impact of disease will be more pronounced when it is coupled to other threats. Although the disease did not increase the probability of extinction of tapirs in Morro do Diabo, it most certainly made the tapir population less resilient to other threats such as fire or road-kill, therefore making it harder for the population to recover from these other threats. This could most certainly compromise the long-term persistence of the tapir population in Morro do Diabo. These results, even being very simple, do suggest that disease can potentially be a significant threat, and efforts should thus be made to investigate the epidemiology of free-ranging tapir populations. An important aspect of assessing disease risk is distinguishing whether the animals actually have a disease or simply harbour or have been exposed to potentially infectious agents. Future tapir health studies must focus on investigating the morbidity and mortality effects of diseases.

6.4.4.4 Tapir Metapopulation Scenario

While Morro do Diabo hosts a rather large tapir population of 126 individuals, the smaller forest fragments in the Pontal do Paranapanema Region fail to provide enough space for more than just a few individuals each. Three of these forest fragments are larger than 10 km^2 and resulted in tapir populations from 4-6 individuals each. Four of the forest fragments are much smaller (4-5 km^2), and did not appear to hold up more than 2 tapirs each (Table 6.4). VORTEX modelling demonstrated that in the absence of dispersal of tapirs from Morro do Diabo, none of the tapir populations in the smaller forest fragments of the Pontal do Paranapanema Region will be viable over the long-term. Without dispersal from Morro do Diabo, all these small tapir populations will go extinct over the next 100 years. However, the dispersal of individuals from Morro do Diabo to the forest fragments had a negative effect on the resident tapir population of Morro do Diabo.

The VORTEX baseline model demonstrated that, in the absence of dispersal, the tapir population in Morro do Diabo would present a population growth of almost 4%. However, a 1% dispersal of tapirs aged from 2-4 years decreased the growth rate of the tapir population in Morro do Diabo to almost 0%. When decreasing the dispersal rate by half (0.5%), the population maintained a population growth rate of 2%. Even when considering a viable tapir population of over 200 individuals (Table 6.5), more precisely 237 tapirs (line-transect estimate), dispersal of tapirs from Morro do Diabo still reduced the growth rate in Morro do Diabo dramatically. In VORTEX, when the initial population size exceeds the carrying capacity at the end of a particular time cycle, additional mortality is imposed across all age and sex classes in order to reduce the population back to this upper limit (Miller & Lacy 2005). Thus, due to their reduced sizes, the small forest fragments in the Pontal do Paranapanema Region are acting as sink habitats for tapirs dispersing from Morro do Diabo and decreasing the stochastic growth rate of the tapir population in Morro do Diabo. Dispersal rate, rather than survival during dispersal or initial population size, was the parameter that had the most impact on the tapir metapopulation in the Pontal do Paranapanema Region.

If the forest fragments were larger and had a potential carrying capacity of 100 tapirs each, the stochastic growth rate of Morro do Diabo would be less impacted as fewer animals would die as a result of lack of habitat carrying capacity. Even so, the fragments still acted as a sink for Morro do Diabo. In general, the VORTEX metapopulation modelling showed that dispersal of tapirs from Morro do Diabo to the forest fragments in the surroundings can be detrimental to the overall metapopulation if the carrying capacity in the fragments is low. Overall, the fragments act as a sink as their initial population sizes are very low. Higher initial populations in the fragments and higher carrying capacity of the fragments would benefit Morro do Diabo and tapir conservation in the Pontal do Paranapanema Region since tapirs from the fragments would act as both source and sink.

6.4.4.5 Corridors: A Potential Conservation Strategy for Tapirs?

Conservation biologists generally agree that landscape connectivity enhances population viability for many species (Gilpin & Soulé 1986; Noss 1987; Primack 1993; Noss & Cooperrider 1994; Hunter 1996; Meffe & Carroll 1997). Because habitat fragmentation often breaks natural connections, many conservationists have advocated the establishment of wildlife corridors in order to promote landscape connectivity. Several authors have argued that corridors can promote the spread of diseases, catastrophic disturbances such as wildfires, introduction of exotic species into the areas connected by corridors, or the luring of animals into areas where they might experience high mortality (Simberloff & Cox 1987; Hobbs 1992; Simberloff *et al.* 1992; Hess 1994). In addition, corridors sceptics have pointed out that the scientific evidence in support of corridors as a conservation tool is very weak, and have objected to the financial costs involved (Simberloff & Cox 1987; Simberloff *et al.* 1992). Nevertheless, corridors are seen as the main landscape element that enhances biological fluxes (Rosemberg *et al.* 1997; Beier & Noss 1998; Haddad & Baum 1999; Tewksbury *et al.* 2002; Orrock *et al.* 2003; Pardini *et al.* 2005; Uezu *et al.* 2005; Damschen *et al.* 2006). In spite of that, the main question surrounding the use of corridors as a conservation strategy still remains: Do corridors enhance or diminish the population viability of target species in the habitat patches connected by them? Any attempts to answer this question must use a species-specific approach.

The VORTEX modelling of the establishment of corridors connecting Morro do Diabo to the surrounding forest fragments in the Pontal do Paranapanema Region reflected an increase in landscape connectivity for tapirs. This increase in landscape connectivity resulted in an increase in stochastic growth rate, which made the tapir populations more resilient to anthropogenic threats, infectious diseases and catastrophes such as fires. Furthermore, it resulted in an increase in percentage of genetic diversity maintained over the long-term, which particularly benefited the smaller tapir populations. Nevertheless, this model implied that rates of tapir mortality were not increased when using corridors. If mortality does occur (*e.g.* dispersing tapirs have to cross a road, or become an easier target for hunters), then the impact of corridors can be very different, and can in fact cause the extinction of the metapopulation. If tapirs using the corridors do not experience increased mortality rates, corridors can be important tools for maintaining long-term genetically viable populations of lowland tapirs in smaller forest fragments as well as in Morro do Diabo.

Chapter 7

Conclusions

&

Conservation Recommendations

Photo by Gilia Angell

7.1 Viability of Lowland Tapir Populations in the Atlantic Forest of the Interior of the Pontal do Paranapanema Region

In this thesis, I used two different approaches to assess the long-term persistence and viability of lowland tapir populations in the Atlantic Forest fragments of the Pontal do Paranapanema Region. The first approach was based on the empirical data collected during this study. This empirical approach focused on aspects of tapir spatial ecology and intra-specific interactions, spatial and temporal interactions between tapirs and the landscape, as well as estimates of tapir abundance, which are all determinant factors for persistence and viability. The second approach consisted of modelling tapir population viability through the use of a computer simulation of Population Viability Analysis. This modelling approach was based on biological characteristics of the species including reproductive and mortality rates.

Lowland tapirs in Morro do Diabo had very large home ranges. Tapir home ranges had remarkably complex internal structures, including multiple core areas of use, which comprised only a very small proportion of the entire home range. These large, complex home ranges were mostly explained by the habitat heterogeneity of the semi-deciduous Atlantic Forests of Morro do Diabo. In addition, the lowland tapir home ranges in Morro do Diabo were considerably larger when compared with previous estimates of home range for the species in large, non-fragmented areas of contiguous habitat (Noss *et al.* 2003; Tobler 2008). This provides evidence that the current tapir home ranges in Morro do Diabo may have been altered by the extensive habitat loss and fragmentation of the Atlantic Forest of the Interior.

Regarding intra-specific interactions, tapirs in Morro do Diabo exhibited extensive home range overlap between neighbouring individuals, including considerably high percentages of overlap between intra- and inter-sexual pairs, as well as between pairs of same and different age classes. Several examples of extensive overlap of core areas of use were also observed. There was no indication whatsoever that spatial territoriality was present in the resident tapir population in Morro do Diabo. While tapirs in Morro do Diabo had very well defined home ranges and lived within their boundaries, no evidence was found that they defended their areas against conspecifics. The patterns of intra-specific interactions observed in Morro do Diabo, particularly home range overlap, were very similar to what has been previously found for the species in non-fragmented habitats.

Concerning habitat requirements, tapirs in Morro do Diabo incorporated varying portions of all available habitat types within their home ranges and core areas of use. In spite of that, tapirs showed strong levels of habitat selection and habitat avoidance. Overall, tapirs strongly selected riparian habitats, and avoided areas of agricultural and pastoral land as well as secondary forest habitats. Tapirs in Morro do Diabo established their core areas of use in riparian forests and performed most of their main activities, especially foraging and resting, in these habitats. This provides evidence that in order to persist over the long-term, besides large home ranges, tapirs also require certain habitat types that contain the resources they need or prefer in order to survive.

Morro do Diabo hosts a rather large and apparently stable, healthy tapir population of ~130 individuals. Results from the Population Viability Analysis projected that a tapir population this size has zero probability of extinction and is likely to persist over the next 100 years even when considering the occurrence of sporadic fire events and a low rate of road-kill. However, this population is not large enough to maintain 95% of genetic diversity over the next 100 years and, therefore, it is not considered to be viable over the long-term. According to the VORTEX model, a Minimum Viable Population of 200 individual tapirs would be necessary to ensure the long-term viability of the tapir population in Morro do Diabo. Thus, there is an urgent need to design and implement conservation strategies for tapirs in Morro do Diabo aiming at promoting an increase in carrying capacity and the maintenance of 95% of genetic diversity. Tapirs have low population growth rates. The modelling exercises that examined the impact of road-kill, infectious disease, and fire on the tapir population of Morro do Diabo, have clearly shown how susceptible this population can be to these threats. These threats would have even more drastic effects for the much smaller tapir populations in the forest fragments.

While Morro do Diabo is the largest Atlantic Forest remnant in the Pontal do Paranapanema Region, the smaller forest fragments are too small to provide enough space for more than just a few individuals each. The largest of the seven forest fragments where the presence of tapirs had been previously confirmed (Santa Maria/Cachoeirinha with 18 km^2), is not large enough to host more than six tapirs according to spatial requirements results from this study. The estimates of tapir population sizes in these small areas resulted in a rather small total number of 22 individual tapirs still surviving in these seven fragments. Altogether, the Atlantic Forests of the Pontal do Paranapanema Region should comprise ~150 tapirs in eight different patches of forest. Unfortunately, these demographic estimates could be potentially overestimated if we considered that tapirs in the smaller forest fragments may not occur at the same density as observed in Morro do Diabo.

This study has gathered strong evidences of tapir movements throughout the fragmented landscape of the Pontal do Paranapanema Region. Tapirs moved fairly easily through areas of non-natural habitat, including fields of agricultural crops and pasture lands. This indicated that the landscape matrix in the Pontal do Paranapanema Region provides a certain level of functional connectivity for these animals. While these movements were observed in relatively short-scales and at low rates, they evidenced a tapir metapopulation scenario. The VORTEX model showed that the maintenance of this metapopulation dynamics might be a determinant factor for the persistence of tapir populations in the Pontal do Paranapanema Region, particularly in the smaller fragments. The tapir populations in the forest fragments are excessively small to persist.

The functioning of the tapir metapopulation in the Pontal do Paranapanema Region is completely dependent on three main conservation factors. The first and most important is that Morro do Diabo must remain intact and effectively protected. The small tapir populations in the forest fragments require recourse to the larger tapir population in Morro do Diabo in order to be demographically and genetically viable over the long-term. Second, the functional connectivity of the landscape matrix in the Pontal do Paranapanema Region must be maintained and, whenever possible, enhanced. Tapirs must be able to move and disperse between different patches of forest. The VORTEX model clearly illustrated this, but also revealed the complexity involved in this measure. Potential mortality rates during dispersal and levels of threats in the unprotected forest fragments being important considerations. The third factor relies on the fact that any threats affecting tapirs in the smaller forest fragments, particularly hunting, must be neutralised. As evidenced by the VORTEX metapopulation model, the tapir population in Morro do Diabo is not large enough to maintain a disrupted "source-sink" structure. It could destabilise the metapopulation and seriously compromise its persistence and viability over the long-term.

7.2 Conservation Recommendations: A First Step in Building a Regional Action Plan for the Conservation of Lowland Tapirs in the Pontal do Paranapanema Region

The results from both the empirical and modelling assessments of the viability of tapir populations in the Atlantic Forest fragments of the Pontal do Paranapanema Region will provide the scientific basis for the design of management and conservation strategies that should be implemented in order to reduce the risk of tapir extinction, and therefore promote their long-term persistence and viability. This is a first step in building a "Regional Action Plan for the Research and Conservation of Lowland Tapirs in the Atlantic Forests of the Pontal do Paranapanema Region." The development of such a plan was, since the beginning, one of the major expected outcomes of this long-term tapir study in Morro do Diabo. Conservation recommendations made here will be used as the foundation for the development of the Regional Action Plan, which will be implemented over the coming years.

Long-term research programmes generate unparalleled amounts of data and information, thus providing the necessary scientific background for the development of comprehensive conservation action plans. Effective conservation planning, particularly when focused on species, can only be done on the basis of a solid scientific knowledge. Therefore, this approach should be potentially very useful for other animal species in other fragmented landscapes worldwide.

7.2.1 Action Planning for Species Conservation

In an effort to save species and overall biodiversity, a number of approaches to conservation have been suggested. Most approaches focused on protected areas, ecosystems, biomes, or other area-based classifications such as "Hotspots" and "Ecoregions" among others. Although critical to conservation, area-based approaches are insufficient on their own. Many wildlife species, and species groups, require species-focused conservation action plans (IUCN 2008b).

Several conservation organisations worldwide have created their own methodologies for the development of species action plans. A few examples include the Population and Habitat Viability Assessment (PHVA), an action planning process developed by the IUCN/SSC Conservation Breeding Specialist Group (CBSG) (Westley & Miller 2003); Range-Wide Priority-Setting and the Landscape Species Approach (LSA), both methodologies designed by the Wildlife Conservation Society (WCS) (Sanderson *et al.* 2002); Conservation Action Planning (CAP) developed by The Nature Conservancy (TNC) (TNC 2007); Habitat Conservation Plan (HCP) developed under the US Endangered Species Act; as well as a number of other species conservation action planning models developed by governmental agencies in range countries. The Species Survival Commission (SSC) of the International Union for Conservation of Nature (IUCN) has been developing Species Action Plans since 1986. In 2006, the Steering Committee of the SSC authorised a Species Conservation Planning Task Force to review all available methods of species-focused conservation planning and prepare a new set of guidelines on strategic planning for species conservation (IUCN 2008b). A handbook has been developed and is now being largely used and, whenever necessary, adapted for the development of local, national, regional and global species action plans.

Action plans are designed to promote species conservation strategies backed by sound scientific information, which is synthesised and translated into prioritised conservation recommendations suggesting realistic solutions attainable by specific actions. These documents are designed for any person or decision-making body that can promote or catalyse conservation action financially, technically, or logistically, influencing key players in the conservation sphere at local, national, regional, and global levels. Action plans provide a common framework and focus for a range of players from decision-makers at the governmental level, to those who will implement the conservation recommendations on the ground. Action plans provide all the information needed to explain why species conservation action needs to be undertaken, including the conservation status of the species, major problems associated with its viability and long-term survival, and what specific actions should be undertaken. An action plan is a "snapshot in time", serving as a baseline set of data and information against which to measure change and monitor progress, indicating where changes of emphasis or direction may be needed to conserve the species. Additionally, action plans identify gaps in species research and policy and give directions for future endeavours through prioritised conservation activities.

7.2.2 Recommendations for the Conservation of Lowland Tapirs in the Atlantic Forests of the Pontal do Paranapanema Region

7.2.2.1 Future Research Priorities and Research Gaps

- **Tapir Population Monitoring: Demography, Epidemiology, and Genetics**
  It is fundamental that the tapir population in Morro do Diabo continues to be closely monitored in the long-term. Now that a very detailed baseline of information is available, it is very important to continuously monitor parameters of population demography, epidemiology and genetics. Population demography should be assessed annually in order to detect any future population fluctuations. In order to do so, it would be advisable to employ a non-invasive, less expensive methodology than radio-telemetry. Regarding epidemiology and genetic monitoring, it would be highly recommended to carry out annual tapir capture rounds aiming at collecting biological samples from tapirs in different areas of Morro do Diabo, including the borders as well as the centre of Morro do Diabo. Future tapir health studies should focus on the study of prevalence of infectious diseases in tapir populations. Furthermore, the morbidity and mortality effects of diseases should be investigated. Population genetics can also be monitored through DNA extracted from tapir faecal samples that can be easily found and collected in the forest. Over the past few years since the tapir telemetry study in Morro do Diabo was concluded, specific genetic markers for lowland tapirs have been developed, tested and made available. Biological samples from all the 35 tapirs captured in Morro do Diabo have been properly preserved for further analyses. In the near future, it will be possible to analyse the relatedness of these 35 individuals and determine the social organisation of tapirs in Morro do Diabo in much more detail. This long-term tapir population monitoring programme should be extended to some of the smaller forest fragments in the Pontal do Paranapanema Region. It would be extremely helpful to obtain estimates of tapir population density in at least some of these areas.

- **Research on Reproductive and Mortality Parameters for Lowland Tapirs**

  The VORTEX sensitivity analysis carried out in Chapter 6 demonstrated that the parameters of sub-adult mortality and adult mortality have the strongest influence on the dynamics of lowland tapir populations. The age of first reproduction for female tapirs appeared to be a sensitive parameter as well. There is virtually no data available on mortality rates, and very little data on reproductive parameters for tapirs in the wild. Therefore, it would be extremely important to design and implement a long-term study to obtain more precise estimates for these parameters that appear to be critical determinants of population persistence and viability. This would allow for an increase in the robustness of the lowland tapir VORTEX model, which would ultimately produce more confident results in the future. This would benefit several other researchers working on lowland tapirs in different parts of the species geographic distribution.

7.2.2.2 Habitat Protection

- **Continuous and Effective Protection of Existing Protected Areas**

  The protected areas in the Pontal do Paranapanema Region, including Morro do Diabo State Park, administered by the Forestry Institute of São Paulo State, and Black-Lion-Tamarin Ecological Station, administered by the Brazilian Federal Agency for the Conservation of Nature and Natural Resources, must remain intact and effectively protected. The administration of Morro do Diabo follows a Management Plan developed and published in 2006. The Black-Lion-Tamarin Ecological Station was created more recently and does not yet have a Management Plan. At any rate, the governmental agencies responsible for the protection of these areas must count on the necessary financial resources to cover the annual operation costs of these protected areas. Considerable amounts of funding are required for the maintenance of infra-structure and effective protection of these protected areas. This includes salaries and benefits for park personnel including a sufficient number of park rangers, maintenance of internal roads and paths, funding for the proper management of buffer zones which includes measures of fire prevention, and prevention of road-kill among many other essential activities.

- **Creation of Private Protected Reserves: *Reservas Particulares do Patrimônio Natural* (RPPN)**

  The Brazilian Atlantic Forest is one of the South American biomes with the highest number of strictly protected areas (parks, reserves, ecological stations, and private reserves) - more than 600 new areas were created during the last 40 years (Galindo-Leal & Câmara 2003). However, the system is far from adequate mostly because these protected areas cover less than 2% of the entire biome, the strictly protected areas

(IUCN categories I and II) protect only 24% of the remnants and, most importantly, most of the remnants are too small (about 75% of protected areas are smaller than 100 km^2) to guarantee long-term species persistence (Tabarelli *et al.* 2005). Much of what is left to preserve in the Atlantic Forest is on private land (Rambaldi & Oliveira 2003), and the establishment of a large and well-designated network of private reserves is now recognised as indispensable for the conservation of this biome. The *Reserva Particular do Patrimônio Natural (RPPN)* is an official protected area category that private landowners can create voluntarily and in perpetuity. There are now 443 RPPNs in the Atlantic Forest domain, totalling almost 1,000 km^2 (Vieira & Mesquita 2004). Several of the small forest fragments in the Pontal do Paranapanema Region would be potential candidates to be converted into RPPNs, which would add to the local network of protected areas, which would most certainly benefit the long-term persistence and viability of populations of tapirs and many other species. Results from the tapir study in Morro do Diabo should be used to identify priority areas to be legally protected. For example, the strong evidence that tapirs select certain habitat types, particularly riparian environments, must be taken into consideration when creating new protected areas. Tapirs require more than just large home ranges for their survival; they require certain habitat types that contain the resources they need. Thus, new protected areas should incorporate these required habitat types.

- **Protection and Restoration of Riparian Habitats**

  In Brazil, the importance of riparian vegetation has been widely recognised, which has led to very strict laws. The Brazilian Forestry Code, a group of laws that regulates the occupation and use of the nation's forests, determined the need to maintain buffer zones of natural vegetation along and around water bodies (Brazilian Environmental Law Nº 4.771/1965). These areas around and along water courses are considered to be "areas of permanent protection" (*Áreas de Preservação Permanente - APP*). The widths of riparian buffers are calculated based upon width and size of the water course. The fact that lowland tapirs in Morro do Diabo strongly selected riparian habitats calls for urgent measures to promote the protection and, whenever necessary, the restoration of these habitats in the Pontal do Paranapanema Region, both inside and outside of protected areas. The law that regulates APPs must be widely and continuously promoted and enforced among private landowners as well as among the state and federal agencies that coordinate the establishment of Agrarian Reform settlements in the region.

7.2.2.3 Habitat Restoration and Re-Establishment of Landscape Connectivity

- **Establishment of Forested Buffer-Zones around Forests Fragments**
  The establishment of forested buffers around Morro do Diabo and other Atlantic Forest fragments in the Pontal do Paranapanema Region should provide an insulative/protective "belt" around fragments, which would most certainly improve habitat quality for tapirs. First, it would increase habitat availability and therefore the habitat carrying capacity. Second, and most importantly, it would mitigate edge effects caused by the process of fragmentation itself as well as by activities of local people. Fire, cattle grazing and spreading of aggressive grasses cause serious damage and gradually erodes the edges of the forests, affecting forest structure. Forested buffer-zones would protect these forest edges from these effects as well as from the wind and the sun, therefore improving the microclimatic conditions of edges. For the successful implementation of forested buffer zones it would be critical to apply the concept of benefit zones. This includes the use of multipurpose trees and shrubs that can be used as valuable resources to families living in Agrarian Reform settlements surrounding the forests of the Pontal do Paranapanema Region. Agro-forestry benefit zones would be another adequate option.

- **Establishment of Wildlife Corridors and Stepping-Stones**
  The establishment of wildlife corridors and stepping-stones connecting Morro do Diabo to the surrounding forest fragments in the Pontal do Paranapanema Region would promote both an increase in habitat availability as well as in landscape connectivity. The increase in habitat availability would increase the carrying capacity for tapirs. The increase in landscape connectivity was modelled in VORTEX and resulted in an increase of the stochastic growth rate of the populations, which should ultimately make these populations more resilient to threats and catastrophes. Furthermore, the model also showed that the increase in landscape connectivity leads to an increase in percentage of genetic diversity maintained over the long-term. Overall, the increase in landscape connectivity appeared to be critical for the long-term persistence and viability of the tapir populations in the region. During this study, 12 possible tapir dispersal routes between Morro do Diabo and surrounding forest fragments, as well as between the fragments amongst themselves, were identified. These tapir pathways should be considered as potential locations for the establishment of corridors and stepping-stones. Once more, for the successful implementation of corridors and stepping-stones, it would be important to apply the concept of benefit zones using multipurpose trees and shrubs and agro-forestry models. Nevertheless, the VORTEX corridor model implied that if tapir mortality rates increased during dispersal then corridors could have a negative impact on the overall metapopulation. Therefore,

measures must be taken to ensure that tapirs will not experience increased mortality when using corridors or stepping-stones. Lastly, it would be advisable to design and establish experiments to monitor the use of corridors by tapirs so that more precise estimates of dispersal rates can be obtained. This would allow for an increase in the robustness of the VORTEX metapopulation and corridor models, which would ultimately produce more confident results in the future.

7.2.2.4 Neutralisation of Threats

The Forestry Institute of São Paulo State and the Brazilian Federal Agency for the Conservation of Nature and Natural Resources must continue to implement effective measures to prevent the occurrence of forest fires in Morro do Diabo and Black-Lion-Tamarin Ecological Station. These measures include the complete clearing of the vegetation, mostly grass, along the edges of Morro do Diabo before and during the dry season, and increased patrolling during the sugar cane burning season. Likewise, the Forestry Institute must continue to employ existing measures to decrease the impact of road-kill on the highway that crosses Morro do Diabo (*SP-613 - Rodovia Estadual Arlindo Bétio*). The speed radars and educational sign posts that were placed on the highway in 2007 have dramatically decreased tapir road-kill and must continue to be used and, whenever possible, improved. Another important strategy would be to enlarge the diameter of six tunnels that already exist under the highway. These tunnels were built during the construction of the highway but are too small to be used by tapirs. Brochures providing information about Morro do Diabo and depicting pictures of road-kill and damaged vehicles should be distributed to all drivers using the road. Posters including the same information and pictures should be placed in local businesses, schools and community centres in all municipalities near Morro do Diabo. Lastly, attention should be given at preventing tapir hunting in the smaller forest fragments of the Pontal do Paranapanema Region. Hunting was most probably responsible for the extirpation of tapirs from some of the forest fragments in the region (Cullen *et al.* 2001a). The Brazilian Environmental Police (*Polícia Ambiental*) should be provided with the proper vehicles, equipment and resources to effectively patrol these areas and enforce the law that forbids hunting of wildlife in the Atlantic Forest biome. Governmental agencies in charge of establishing and managing Agrarian Reform settlements should be involved and contribute to the process. Current environmental education initiatives carried out by IPÊ - Instituto de Pesquisas Ecológicas and other conservation organisations working in the Pontal do Paranapanema Region must address the issues of fire, road-kill and hunting in their educational activities and materials.

7.2.2.5 Tapir Management: Translocations and Re-Introduction

Translocation and re-introduction could potentially become useful tools for the management and restoration of tapir populations in severely fragmented landscapes such as the Atlantic Forest. The four species of tapirs are good candidates for translocation and re-introduction programmes. Previous studies have shown that ungulate translocations have high success rates (Shepherdson 1994). Studies have further revealed that tapirs are adaptable to changes in diet and environmental conditions (Brooks *et al.* 1997), and hence have the potential to successfully overcome some of the greatest challenges presented to relocated animals. Nevertheless, it is fundamental that we learn how to use these techniques properly. Thus, it would be useful to design and establish tapir translocation and re-introduction experiments. These experimental tapir translocations and re-introductions should follow and test the appropriateness of the Guidelines for Tapir Re-Introductions and Translocations (Medici *et al.* 2008), recently published by the IUCN/SSC Tapir Specialist Group (TSG). Initially, candidate animals should be tapirs confiscated from illegal owners or traders, or displaced by habitat loss (*e.g.* filling of dams, deforestation, sugar cane burning fields, forest fires). Local zoos, breeding centres and wildlife rehabilitation centres could be potential sources of animals. It would be advisable to start with small-scale translocations and re-introductions in release sites where tapirs are not present. Other factors that should be considered when selecting release sites include: area carrying capacity (*e.g.* presence of large patches of fruiting plant species, large water bodies and riparian habitats), threats (it is critically important that the causes of local tapir extinction are no longer in place), conservation category of release site (protected area, private reserve), presence/absence of predators (large cats), genetic and health assessments, possible ecological effects of tapirs in the area, logistic concerns, participation of local communities among others. Availability of personnel and funding are critical aspects that must be considered when establishing such experiments. These experiments should be used to gather baseline information for future large-scale, long-term translocation and re-introduction programmes aiming at restoring tapir populations.

7.3 Determinants for Long-Term Persistence of Animal Populations across Fragmented Landscapes

Worldwide, tropical forests are increasingly threatened by escalating human population and the resulting conversion for agriculture, cattle ranching and urban development. Habitat destruction and fragmentation are considered to be the primary causes of the present species extinction crisis (Wilcox & Murphy 1985; Gibb & Hochul 2002; Schmiegelow & Monkkonen

2002; Vié *et al.* 2009). The underlying question proposed by this thesis was: What are the ecological factors that determine the survival and long-term persistence of animal populations in severely fragmented landscapes? Lowland tapirs and the fragmented Atlantic Forests of the Interior of the Pontal do Paranapanema Region, São Paulo State, Brazil, were used as a model to illustrate and answer this question.

The long-term persistence and viability of animal populations across severely fragmented landscapes is strongly determined by life-history parameters (*e.g.* body size, reproductive cycles, and generation length among others). These will determine the species ability to recover after severe decreases. Other determinant factors are species spatial requirements and population sizes. Aspects of patch size and availability of required habitat types, as well as landscape composition, connectivity and the species capability to disperse, are equally important. Lastly, the level of protection of forest patches and the impact of existing threats to the target species are also determinant factors.

Animal populations across fragmented landscapes, particularly wide-ranging species with large spatial requirements such as tapirs, are usually found in small sizes. The abundance and predictability of food resources both in time and space are particularly limited in fragmented landscapes. Survival and reproduction are food-limited. In fragmented areas, animals must be capable of adapting and acquiring a certain level of behavioural plasticity, most particularly with regards to spatial and habitat requirements. Animals in fragmented patches of forest likely need larger home ranges in order to find sufficient food and other vital resources to survive and persist. The smaller and more degraded the forest patch, the more space animals will need to fulfil their resource requirements. Overall, fragmented habitats usually fail to provide these resources, which in turn leads to a general reduction in the number of individuals that can be hosted in a given area (Lovejoy *et al.* 1984; Quinn & Hastings 1987; Bierregaard *et al.* 1992; Burkey 1993; Kattan & Alvarez-Lopez 1996).

Population size is the major determinant of species capacity for long-term persistence and viability (Diamond *et al.* 1987; Newmark 1987; Pimm *et al.* 1988; Richman *et al.* 1988; Soulé *et al.* 1988; Berger 1990; Schoener & Spiller 1992; Foufopoulos & Ives 1999). Small, isolated populations are more sensitive to stochastic events, such as fires or epidemic outbreaks (Lacy 1993; Lacy 2000; Aurambout *et al.* 2005) as well as to genetic drift (Templeton *et al.* 1990). All these factors can very rapidly drive an animal population to extinction. Similarly, losses of habitat quality in forest fragments are important causes of species extinctions (MacArthur & Wilson 1967; Gilpin & Soulé 1986; Wilcove *et al.* 1986; Terborgh 1992). Hence, in addition to area restrictions and small population sizes, factors related to habitat quality will also affect the persistence of animal populations in forest fragments.

As demonstrated by the tapirs in this study, animals usually show selection or avoidance for different types of habitat found within their home ranges. By selecting a certain habitat type, an animal attempts to maximise its survival, reproductive success, and the net rate of energy intake (Johnson 1980; Abrams 2000; Delibes *et al.* 2001). Presumably, species should survive and reproduce better (*i.e.* their fitness should be higher) in habitats that they select (Rosenzweig & Abramsky 1986). The existence of patches of selected habitats is fundamental for the long-term persistence of a healthy, functioning population.

As a consequence of the combination of all the factors described above, for most animal species, small populations in fragmented landscapes may not be able to persist and be viable over the long-term unless a certain level of landscape connectivity exists. Connectivity is a vital parameter for the persistence of animal species in severely fragmented landscapes (Karr 1982; Blake & Karr 1987; Bierregaard & Stouffer 1997; Stratford & Stouffer 1999; Crooks *et al.* 2000; Uezu *et al.* 2005). While patch size is mainly related to the probability of local extinction (Levins 1970; Hanski & Gilpin 1997), connectivity is associated with migration rates, and thus with the (re)colonisation probability and the rescue effect (Uezu *et al.* 2005). Landscape connectivity facilitates biological fluxes by allowing animals to move and disperse in between patches of forest. This is critical for the maintenance of metapopulation dynamics, which in fragmented landscapes is a major determinant for the resilience of animal populations to catastrophes and threats, as well as for the maintenance of genetic diversity. Results from this tapir study in the Pontal do Paranapanema Region demonstrated that tapirs move fairly easily through areas of non-natural habitat in between forest fragments and that this is extremely important for the long-term survival of tapir populations in the region. Functional connectivity depends not only on the landscape pattern, but also on the interactions between this pattern and the biological characteristics of the target species, such as their ability to move through areas of non-natural habitat (Greenberg 1989; Sieving *et al.* 1996).

Animal responses to habitat alteration and fragmentation are species-specific. Some taxa are more affected by fragment size, while others by landscape connectivity. Limited dispersal capacity of certain species may be a key factor determining their sensitivity to fragmentation (Sekercioglu *et al.* 2002), as well as their ability to persist over the long-term. Regarding connectivity, some species may be more sensitive to inter-patch distance, whereas others are more sensitive to the presence of corridors (Uezu *et al.* 2005). These different perceptions are particularly relevant since they can elucidate which landscape components play major roles for the viability of each animal species. Large animals such as tapirs are highly mobile and likely have a greater perceptual range (Zollner 2000), thereby being able to detect suitable habitat and perceive landscape structure and interrelatedness (Wiens 1996). Smaller, less mobile animal species with more restricted ranges may not be capable of doing so and may thus require more intense landscape management, such as the establishment of corridors or stepping-stones, or the employment of animal management techniques, such as translocations, re-introductions, or managed dispersals, in order to persist and be viable over the long-term. At any rate, even low levels of dispersal in between patches of forest may be sufficient to maintain small populations in sink areas (Pulliam 1988), as long as potential sources of dispersers exist (Novaro *et al.* 2000). The quality of the intervening non-habitat matrix for the survival of dispersing individuals is particularly important (Fahrig 2001) given that increased mortality during dispersal outweighs the potential positive effect of dispersal on metapopulation dynamics (Gibbs 1998; Fahrig 2001).

Results from this tapir study have shown that non-protected forest fragments in the Pontal do Paranapanema Region continue to suffer from habitat degradation in many different ways, which leads to a continuous reduction in habitat quality and consequently carrying capacity for tapirs. The effective protection of existing parks and reserves as well as the creation of new protected areas including patches of required habitat types could have a major impact in promoting the persistence of animal species. Furthermore, the impact of different threats affecting different species (*e.g.* hunting, road-kill, fire, infectious disease, tourism, construction of infra-structure among many others) must be addressed and, whenever possible, neutralised. While habitat destruction and fragmentation lead to small, isolated populations, lowland tapirs in the fragmented Atlantic Forests of the Interior of the Pontal do Paranapanema Region showed that other threats override the impact of fragmentation. Threats can rapidly accelerate the likelihood of extirpation of remaining small animal populations. Disrupted source-sink structures can seriously destabilise metapopulation dynamics and compromise the long-term persistence and viability of animal populations.

In conclusion, the long-term persistence and viability of animal populations across severely fragmented landscapes completely depends on the maintenance and full protection of complex landscape networks. These networks must include some large patches of habitat that can host larger animal populations and function as sources of dispersers for smaller populations in sink habitats. In addition, patches composing these landscape networks must incorporate required habitat types where animals can find the resources they need in order to survive. Lastly and most essentially, there must be an appropriate level of landscape connectivity, either structurally or functionally, in order to allow for biological fluxes between patches and for the maintenance of a demographically and genetically healthy metapopulation.

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Appendix I. Timeframe of different activities carried out during the long-term lowland tapir research study in Morro do Diabo State Park, São Paulo, Brazil, from 1996-2008, including field work, data analysis and fundraising activities.

Activity	1996	1997	1998	1999	2000	2001	2002	2003	2004	2005	2006	2007	2008
Initial tests of appropriate radio-transmitter attachments	▨												
Tapir captures for radio-tagging and collection of biological samples		▨	▨		▨	▨	▨	▨	▨				
Radio-telemetry monitoring of 19 radio-collared tapirs			▨	▨	▨	▨	▨	▨	▨	▨	▨		
Collection of faecal samples for genetics, epidemiology and diet studies								▨	▨	▨			
Tapir captures for epidemiological and genetics monitoring											▨	▨	▨
Nocturnal line-transect sampling data collection											▨	▨	▨
Data collection for the FIT reference library										▨	▨		
Data collection for application of the FIT in the wild												▨	
Development of the lowland tapir baseline model for VORTEX											▨	▨	
Data analysis											▨	▨	▨
Fundraising and reporting	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨

Appendix II. Complete information about 35 lowland tapirs (20 females and 15 males, or 27 adults, 6 sub-adults, and 2 juveniles) captured from June 1996 to July 2008 in four different sections of Morro do Diabo State Park, São Paulo, Brazil. Animal identification (ID), date of capture (dd.mm.yyyy), capture site (WB: West Border, SB: Southeast Border, NB: Northwest Border, CE: Centre, Figure 3.1), sex (F: female, M: male), age (A: adult, SA: sub-adult, J: juvenile), timeframe of monitoring (LT: long-term, ST: short-term, NM: not monitored, number of months), and general notes (predation, recapture, mortality, loss of collar) are shown.

Animal ID	**Date of Capture** dd.mm.yyyy	**Capture Site**	**Sex**	**Age Class**	**Monitoring**	**Period of Radio-Tracking** (months)	**Note 1**	**Note 2**
Joana	24.06.1997	WB	F	A	Radio-Collared - LT	36	Mortality record (Aug2000, natural causes)	
Paulete	21.01.1998	WB	F	A	Radio-Collared - LT	33		Recaptured in 25.03.2000
Docinho	21.01.1998	SB	F	A	Radio-Collared - LT	22		Recaptured in 15.11.1999, 10.7.2000
Luizinho	14.07.1998	WB	M	SA	Radio-Collared - ST	3	Mortality record (Oct1998, predated by puma)	
Chu-Chu	23.07.1998	WB	F	SA	Radio-Collared - LT	35		
Batista	28.07.1998	CE	M	A	Radio-Collared - NM		Collar fell off right after the capture	
Xuxa (+calf)	31.07.1998	WB	F	A	Radio-Collared - ST	3	Collar stopped working 3 months after the capture	
Gringo	11.12.1998	SB	M	A	Radio-Collared - NM		Collar fell off right after the capture	
Marinho	05.07.2000	WB	M	SA	Radio-Collared - NM		Collar fell off right after the capture	
Mikilique	10.07.2000	SB	M	A	Radio-Collared - NM		Collar fell off right after the capture	
João	11.07.2000	WB	M	SA	Radio-Collared - ST	2	Mortality record (Sep2000, predated by jaguar)	
Patrícia	17.07.2000	WB	F	SA	Radio-Collared - LT	30		Recaptured in 23.07.2008

Sem Nome	14.01.2001	SB	M	A	Radio-Collared - NM		Collar fell off right after the capture	
James Bond	17.01.2001	SB	M	A	Radio-Collared - LT	29		
Georgete (+calf)	18.01.2001	SB	F	A	Radio-Collared - LT	25		Recaptured in 10.11.2003
Dedinho	16.01.2002	NB	M	A	Radio-Collared - ST	2	Collar fell off 2 months after the capture	
Esperta	20.01.2002	NB	F	A	Radio-Collared - LT	22	Mortality record (Nov2003, predated by jaguar)	
Baby	10.04.2003	CE	F	A	Radio-Collared - ST	4	Collar fell off 4 months after the capture	
Cicinho	01.06.2003	CE	M	A	Radio-Collared - NM		Mortality record (25 days after capture, natural causes)	
Chico	25.06.2003	CE	M	A	Radio-Collared - LT	28		Recaptured in 22.07.2008
Júlia	01.07.2003	CE	F	A	Radio-Collared - LT	12		Recaptured in 29.07.2004
Cidão	14.04.2004	CE	M	A	Radio-Collared - LT	8		
Tonha	19.04.2004	CE	F	A	Radio-Collared - LT	33		
Tina	27.04.2004	CE	F	A	Radio-Collared - LT	27		Recaptured in 19.07.2006
Mama	19.05.2004	CE	F	A	Radio-Collared - LT	18		Recaptured in 05.01.2007
Tunga	11.07.2006	CE	F	A	Epidemiology/Genetic			
Joares	13.07.2006	CE	M	A	Epidemiology/Genetic			
Diana	08.01.2007	CE	F	A	Epidemiology/Genetic			
Cris	12.01.2007	SB	F	A	Epidemiology/Genetic			
Gatinho	18.01.2007	CE	M	SA	Epidemiology/Genetic			
Branquinha	02.06.2007	CE	F	A	Epidemiology/Genetic			
Volverina	07.06.2007	CE	F	A	Epidemiology/Genetic			
Regininha	10.06.2007	CE	F	J	Epidemiology/Genetic			
Fêmea 08JL	20.07.2008	CE	F	A	Epidemiology/Genetic			
Robinho	20.07.2008	CE	M	J	Epidemiology/Genetic			

Appendix III. Timeframe of radio-tracking of 19 tapirs (13 females and 6 males, or 15 adults and 4 sub-adults) monitored in four sections of Morro do Diabo State Park, São Paulo, Brazil. Value in () is the total number of months of radio-tracking of each radio-collared tapir.

Year/ Month		**West Border**							**Southeast Border**			**Northwest Border**		**Centre**						
		JOAn	**PAU**	**LUI**	**CHU**	**XUX**	**JOAo**	**PAT**	**DOC**	**JAM**	**GEO**	**DED**	**ESP**	**BAB**	**CHI**	**JUL**	**CID**	**TON**	**TIN**	**MAM**
1997	J	1																		
	A	2																		
	S	3																		
	O	4																		
	N	5																		
	D	6																		
1998	J	7																		
	F	8	1						1											
	M	9	2						2											
	A	10	3						3											
	M	11	4						4											
	J	12	5						5											
	J	13	6	1					6											
	A	14	7	2	1	1			7											
	S	15	8	**(3)**	2	2			8											
	O	16	9		3	**(3)**			9											
	N	17	10		4				10											
	D	18	11		5				11											
1999	J	19	12		6				12											
	F	20	13		7				13											
	M	21	14		8				14											
	A	22	15		9				15											
	M	23	16		10				16											
	J	24	17		11				17											
	J	25	18		12				18											
	A	26	19		13				19											
	S	27	20		14				20											
	O	28	21		15				21											
	N	29	22		16				**(22)**											
	D	30	23		17															

2000	J	31	24		18															
	F	32	25		19															
	M	33	26		20															
	A	34	27		21															
	M	35	28		22															
	J	**(36)**	29		23															
	J		30		24															
	A		31		25		1	1												
	S		32		26		**(2)**	2												
	O		**(33)**		27			3												
	N				28			4												
	D				29			5												
2001	J				30			6												
	F				31			7		1	1									
	M				32			8		2	2									
	A				33			9		3	3									
	M				34			10		4	4									
	J				**(35)**			11		5	5									
	J							12		6	6									
	A							13		7	7									
	S							14		8	8									
	O							15		9	9									
	N							16		10	10									
	D							17		11	11									
2002	J							18		12	12	1								
	F							19		13	13	**(2)**								
	M							20		14	14									
	A							21		15	15									
	M							22		16	16									
	J							23		17	17		1							
	J							24		18	18		2							
	A							25		19	19		3							
	S							26		20	20		4							
	O							27		21	21		5							
	N							28		22	22		6							
	D							29		23	23		7							

2003	J							**(30)**		24	24		8							
	F									25	**(25)**		9							
	M									26			10							
	A									27			11	1						
	M									28			12	2						
	J									**(29)**			13	3	1					
	J												14	**(4)**	2	1				
	A												15		3	2				
	S												16		4	3				
	O												17		5	4				
	N												18		6	5				
	D												19		7	6				
2004	J												20		8	7				
	F												21		9	8				
	M												**(22)**		10	9				
	A														11	10	1	1		
	M														12	11	2	2	1	1
	J														13	**(12)**	3	3	2	2
	J														14		4	4	3	3
	A														15		5	5	4	4
	S														16		6	6	5	5
	O														17		7	7	6	6
	N														18		**(8)**	8	7	7
	D														19			9	8	8
2005	J														20			10	9	9
	F														21			11	10	10
	M														22			12	11	11
	A														23			13	12	12
	M														24			14	13	13
	J														25			15	14	14
	J														26			16	15	15
	A														27			17	16	16
	S														**(28)**			18	17	17
	O																	19	18	**(18)**
	N																	20	19	
	D																	21	20	

2006	J																	22	21	
	F																	23	22	
	M																	24	23	
	A																	25	24	
	M																	26	25	
	J																	27	26	
	J																	28	**(27)**	
	A																	29		
	S																	30		
	O																	31		
	N																	32		
	D																	**(33)**		