# UNIVERSITY OF SOUTHAMPTON

FACULTY OF MEDICINE, HEALTH AND LIFE SCIENCES

SCHOOL OF BIOLOGICAL SCIENCES

# The use of camera traps for estimating abundance and studying the ecology of jaguars (*Panthera onca*)

by

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## ABSTRACT
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## TITLE OF THESIS: THE USE OF CAMERA TRAPS FOR ESTIMATING ABUNDANCE AND STUDYING THE ECOLOGY OF JAGUARS (*Panthera onca*)
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The use of camera trap data in mark-recapture analyses to estimate mammal abundance is becoming increasingly popular as a non-invasive technique to study cryptic species. To date there has been no scientific scrutiny of the reliability of such estimates or any investigation into the required trapping effort and optimal distribution of traps. The present study addresses these issues using estimates of jaguar (*Panthera onca*) abundance in the secondary moist broadleaf forest of the Cockscomb Basin Wildlife Sanctuary (CBWS), Belize. A total of 645 captures of jaguars (37 individuals), 608 captures of pumas (*Puma concolor*) and 1603 captures of prey species, were used for this study. The study also investigates the limits to which camera trap data can be used to answer ecological questions about the target species.

Simulation models were used to identify the threshold of capture rate and heterogeneity of capture rate below which estimates were found to be unreliable. Most published studies fell below this threshold of $\geq 0.05$ catchability. Here we report the first long-term camera trap study with multiple surveys. Re-sampling the survey data showed that abundance estimates could be biased by variation in survey length and minor changes in camera locations. A wider distribution of cameras gave more reliable abundance estimates compared to a concentrated distribution for a fixed number of cameras, provided optimal locations were used. Locations that optimised jaguar capture rate were associated with wide, established trail systems. This study presents guidelines to improve the reliability of abundance estimates.

Camera trap data were used for the first time to test hypotheses about the mechanisms of coexistence of jaguars and pumas and about the social system of jaguars by investigating their spatio-temporal distribution. It was shown that jaguars and pumas were predominantly nocturnal with substantial inter-specific spatial overlap but did not occupy the same space at the same time. It was also found that jaguars leave forest trails more frequently than pumas. Jaguar captures were strongly biased towards males, due in part to males being more active and moving further than females. The spatial distribution of male jaguars was characterised by extensive range overlap. There was no stability in occupancy, or evidence of avoidance between males.

The role of scrape-marking behaviour in jaguar and puma social systems was investigated. Scrapes were clustered along trails in spatially stable ‘hot-spots’. Monitoring through time revealed that scrapes elicit counter-scraping nearby, probably by conspecifics. Camera data showed that scrapes were mostly associated with puma captures. There was no evidence that higher scrape frequencies were associated with particular individuals.

Combined sign and camera surveys were deployed to investigate whether camera trap data can measure the relative abundance of prey species of jaguars and pumas. Prey species varied greatly in their use of trails, rendering camera traps unreliable for applications to prey. A total of 450 scats were collected over 3 years to determine jaguar and puma diet. This is one of the largest diet studies on large neotropical cats. Spatial and temporal variation in diet was found across the CBWS, indicating that short-term diet studies in small areas should be interpreted with care.

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# Chapter 1

# Conservation and ecology of large neotropical cats

# Introduction

Over the last few centuries species extinctions have been accelerated by anthropogenic factors (Wilson 1992, Kerr & Currie 1995, Lande 1998). Habitat fragmentation prevents the maintenance of viable connected populations and often species cannot adapt fast enough to the human induced environmental changes (Estrada et al. 1993, Estrada & Coates-Estrada 1996, Lande 1998, Purvis et al. 2000, Shafer 2003, Travis 2003, Cardillo et al. 2004). In situ conservation of viable and connected populations of target species has become more complex as the growing human population competes for space and resources (Wilson 1992, Lande 1998, Cardillo et al. 2004). Often economic development conflicts with the preservation of land; conservation must be supported by reliable data so that the few areas and resources that society is willing to conserve have the maximum conservation effectiveness.

Land lies at the heart of the conflict between wildlife conservation and human development (Wilson 1992, Lande 1998, Diniz et al. 2005) therefore the most difficult species to preserve but most in need of conservation are those that require large continuous areas of land for their individual survival, like most larger mammals (Purvis et al. 2000, Diniz et al. 2005). Large terrestrial carnivores are at the top of the trophic pyramid and so are ideal umbrella species for conservation (Carroll et al. 2001, Sergio et al. 2006). They often eat wide ranging herbivores and so are among the widest ranging terrestrial animals. 75% of carnivorous mammals of ≥ 20 kg are threatened or near threatened (IUCN red list 2006). Ecosystems that support large terrestrial mammals are relatively rich in biomass and often reflect regional scale population processes (Carroll et al. 2001). The conservation of large mammalian carnivores will therefore ensure the conservation of many species living lower down the trophic pyramid, thus the carnivore functions as an “umbrella species” for the conservation of others (Carroll et al. 2001, Sergio et al. 2006).

Conservation science aims to provide reliable data for effective conservation planning. Carnivore conservation is hindered by the lack of such data. Their cryptic nature makes them difficult to study preventing basic predictions about survival or population dynamics necessary to make policy. Methods to study such species need to be developed, tested and then utilised to collect reliable data.

The jaguar *(Panthera onca)* is an example of a mammalian carnivore that has eluded scientific study for decades. Little is known of its natural history, distribution or abundance. The habitat in which it lives, mostly neotropical rainforest, the low density at which it lives and its cryptic lifestyle make it one of the most difficult mammals to study.

This study was designed to optimise current methods for studying elusive forest mammals using the jaguar as the target species. The suitability of the methods for answering ecological questions about the jaguar is explored with the main emphasis on estimating abundance. To highlight the need for new methodologies, current understanding of jaguar biology will be presented in this chapter. Where information about jaguars is lacking information from other large cat species will provide the theoretical framework. The objectives of this chapter are:

1) to discuss conservation of the large neotropical cats.

2) to outline current understanding of the ecology and behaviour of the large neotropical cats as is relevant to subsequent data chapters (distribution, spatial and temporal patterns of coexistence within and between species, hunting behaviour, diet and social system).

3) to summarise the data chapters of this study (Chapters 3 - 9).

## Critical issues for the conservation of large cats

Two large felids inhabit the neotropics, the jaguar and the puma (*Puma concolor*), both face direct persecution, habitat loss and prey depletion, exemplifying the current threats challenging all large tropical carnivores. Both with a population of ~50, 000, they are “near threatened” and are likely to be upgraded to “vulnerable” if more data are available and current threats are not mitigated (IUCN Red List 2006). During the peak of the fur trade in the 1960s up to 10,000 jaguar pelts were exported per year (Rabinowitz 2006), suggesting that until fairly recently the jaguar population was much larger than it is today. The fur trade remained the main threat to jaguars until 1970’s when it was outlawed by international convention (Convention on International Trade in Endangered Species, 1973, CITES). Enforcement of CITES in Europe and the USA has reduced the trade in jaguar pelts.

## Are protected areas large enough to safeguard the large cats?

The survival of most large carnivores depends on protected areas and in many parts of the world protected areas are established with this sole purpose. Tigers (*Panthera tigris*) are rare outside protected areas. There are estimated to be 4000 to 6000 tigers in the wild, distributed over 14 countries (Nowell & Jackson 1996). Their habitat is fragmented into a few small islands of protected areas within an ocean of developed land. Few of these protected areas are connected and most are individually too small to sustain a tiger population in the long term (Nowell & Jackson 1996).

Compared to the tigers in Asia, the situation is more positive for big cats in the neotropics. Although there are few protected areas large enough to sustain a jaguar or puma population they can live outside protected areas in as yet undeveloped wilderness areas. Pressure for land and resources is less extreme in Latin America than in Asia. Conversion of wilderness areas into farm and urban area has been more extensive in Asia where there are 423 people / $km^2$ of agricultural land compared to 58 people / $km^2$ in Latin America (Bryant 2002). However the annual growth rate of the human population is greater in Latin America than Asia and this is likely to accelerate habitat loss in Latin America (1.9% Latin America, 1.8% Asia, Bryant 2002).

The conservation community needs to plan ahead to safeguard the future of the neotropical large cats in order to avoid the hopeless situation faced by tigers. The reality of the situation is that protected areas, although an extremely important tool, will never be sufficient for the conservation of large cats in Latin America. Co-existence between big cats and humans in marginal cultivated habitats will have to be part of the solution.

## Threats: habitat destruction

Forest is the dominant habitat type of the jaguar and logging can form an important part of the local economy. Logging is not necessarily detrimental to large terrestrial carnivores, which mainly rely on terrestrial prey. Selective logging creates a mosaic of open areas within the forest. This can promote terrestrial herbivores and thus support a higher density of carnivores. For example, tiger densities are low in the tropical forests of South East Asia but high in India in areas that used to be maharaja hunting grounds: forested areas with large grassland clearings. Such a mosaic landscape supports an abundance of grazers and browser herbivores, perfect for carnivores (pers. obs. B. J Harmsen, thesis author). The Cockscomb Basin in Belize was heavily logged during the 1980's but has been protected since 1986. The secondary forest supports one of the highest densities of jaguars in the world (Rabinowitz & Nottingham 1986; Silver et al. 2004).

Large-scale overexploitation of plant species is unlikely to have a negative impact on large terrestrial carnivores even if the habitat is greatly altered, for example conversion of primary to secondary forest or endangerment of certain tree or plant species (e.g. extraction of mahogany trees (*Swietenia macrophylla*) or xate palm (*Chamaedorea spp.*)). However, the secondary effects of human colonisation do pose a threat.

## *Threats: direct persecution*

Large cats have always faced direct persecution from man. They can sustain intensive persecution for short periods because lowered density increases the survival of the remaining individuals, particularly cubs. For example, jaguars have recovered since the fur trade ceased, and populations are increasing in many range countries where habitat is suitable (pers. comm. A. Rabinowitz, director of science and exploration, Wildlife Conservation society). Puma populations can withstand an annual harvest of 10-25% of the total population as long as habitat and prey populations are adequate (Lindzey et al. 1992, 1994). Tiger numbers in India doubled within 10 years of the establishment of several large tiger reserves (Nowell & Jackson 1996). Female tigers reproduce quickly after loss of cubs and cub survival rates are high in areas with sufficient prey (Sunquist et al. 1999). However the current long term persecution of tigers, due to their high black market value in Asia, is too intense to allow recovery of the tiger population (Hemley & Mills 1999).

Inaccessibility may lower the threat of direct persecution. Hunters often only travel one or 2 days by foot into the forest therefore extensive areas are protected by their size alone, even if legal protection is minimal and hunting motivation is high (pers. obs, B. J Harmsen, thesis author). Species are more vulnerable in open accessible areas. For example the areas from which jaguars have been extirpated are characteristically open: the pampas of Argentina and large parts of the cerrado grasslands of Brazil (Sanderson et al. 2002). Also, large predators of the open lands of the African savannah, such as spotted hyaenas (*Crocuta crocuta*) and lions (*Panthera leo*), are rare outside protected areas (Nowell & Jackson 1996).

Logging operations create roads and thus facilitate human activity, including hunters. For example, in the Congo logging roads open up new areas for bush meat hunters which may lead to the total annihilation of populations of large mammals (Wilkie et al. 2000). In Russia, proximity to roads has a substantial effect on the survival rate of Siberian tigers. Kerly et al. (2002) found evidence that all breeding females died prematurely because of human interference (mainly poaching) compared to areas where there were no roads. Furthermore, in areas where there were primary roads tigers spent less time at a kill site than tigers in undisturbed areas. In Africa partnerships are now being established between logging companies and conservation organisations in which the logging company agrees to destroy the road network before leaving the area (pers. comm. L. Ostro, head of development, Wildlife Conservation Society).

## *Threats: competition with humans*

In areas where bush meat is the main source of protein, humans hunt opportunistically and large predators can provide both meat and financial gain because of the economic value of the bones or skin (Hemly & Mills 1999). In such scenarios, in which both the predator and their prey species are hunted by humans, it is unlikely that the predator will rebound from persecution.

Densities of carnivores are often closely linked to the densities of their prey, for example, tiger density has a linear relation with prey biomass (Sunquist et al. 1999). Carnivores such as tigers show a preference for the larger prey species such as large cervids compared to smaller species such as muntjac (*Muntiacus muntjak*) and wild boar (*Sus scrofa*), since these larger species yield the highest ratio of energy gained to effort expended; in particular a mother with cubs will rely heavily on large animals in order to feed herself and her off-spring with a single kill (Sunquist et al. 1999).

Human hunters show a similar preference as the large cats; the large cervids, wild pigs and bovines are all favoured game. In areas of South East Asia, where hunting is extensive, large sambar deer (*Cervus unicolor*) live at extremely low densities and tigers now have to rely mainly on smaller deer such as muntjac (Rabinowitz & Walker 1991). The hypothetical scenario of "muntjac only diet" could sustain a tiger but breeding is not possible since a tigress would not be able to feed her cubs (Sunquist et al. 1999). Models predict that prey depletion will lower tiger long term survival more than direct persecution (Karanth & Stith 1999).

Prey species in the Neotropics are smaller than those in Asia. The largest mammals are small deer, wild pigs (peccaries) and large rodents. They are important prey for both jaguars and pumas and are also heavily hunted by humans throughout the region (Novack et al. 2005).

Wild meat consumption can have a major impact on local mammal composition (e.g. Fa et al. 2000), directly affecting carnivore survival. Prey depletion may also increase the level of risk that a carnivore has to take in order to find sufficient prey. This can increase vulnerability to direct persecution, particularly if it leads to predation on domestic livestock.

In Chapter 7 methods to measure prey availability in the neotropics will be discussed. In Chapter 8 the diet of jaguars and pumas will be discussed in more detail.

## *Threats: direct conflict with humans*

Habitat loss increases the contact zone between humans and carnivores, often bringing them into direct conflict. For example, tiger reserves are surrounded by intensive human development (agriculture and urban areas). Since the tiger population cannot exceed the carrying capacity of the reserve, dispersing individuals are likely to come into conflict with humans (Nowell & Jackson 1996).

Carnivores often hunt both wild prey and domestic animals at the edge of protected areas or in areas where humans have recently cleared the land. Prey depletion due to over-hunting by humans will exacerbate the problem. For example, in most parts of their range snow leopards (*Uncia uncia*) now depend on domestic animals because overgrazing by livestock and over-hunting has reduced the wild prey populations such that there is not enough to sustain the snow leopard population (Nowell & Jackson 1996). Any short term conservation of viable snow leopard populations will have to take into account that these cats depend almost entirely on livestock to survive. High levels of livestock predation by jaguars are associated with low wild prey densities (Linnell et al. 2002, Polisar et al. 2003, Conforti & Azevedo

2003), whilst Miller (2002) describes a case of jaguars and cattle co-existence in the absence of livestock predation in an area with high prey density.

All large cats pose a threat to humans, whether real or perceived, either directly or to their livelihood; consequently it is difficult to convince people living within the cats' range that they should be protected. Some species such as lions in Africa and tigers in India are easily visible and have an economic value in the eco-tourism trade. However most large cats, such as jaguars and pumas, are elusive and so their protection will do little to boost the local economy.

Although jaguars and pumas are protected, they are regularly killed by livestock owners. This may range from a reactive response, hunting cats only when there has been a livestock kill, to a pro-active "shoot on sight" policy (pers. comm. R. Foster, PhD student, Southampton University). Attitudes towards cats can be positive in an area despite regular persecution (Conforti & Azevedo 2003). In Belize attitudes towards jaguars were generally positive yet livestock owners readily admitted killing them (Brechin & Buff 2005).

## ***What are the survival prospects of large neotropical cats?***

The conservation of jaguars and pumas is multifaceted and complicated. Availability of prey is one of the most important issues. Reduction in wild prey can force cats to prey on domestic animals and come into direct conflict with humans. The cats can tolerate a certain level of habitat conversion if wild prey species are abundant, for example pumas in the USA (Lindzey et al. 1992). In other areas wild prey are important protein sources for the local human population, for example, in the Atlantic forests of Brazil, where jaguars and pumas are seriously threatened, intensive cultivation has fragmented the landscape and both cats are in direct competition with man for the prey in the remaining forest fragments (Garla 2001).

There is no single answer to conserving the large cats of the neotropics. Specific solutions must be targeted at local problems. The first step is to identify the areas that are important for jaguar and puma conservation. Currently this is hindered by lack of data on cat distribution. Sanderson et al. (2002) attempted to identify priority areas for jaguar conservation. However their data are based mainly on "expert opinion", which is often little more than a best guess. Quantitative data from a number of locations are required, to estimate jaguar and puma abundance in different areas.

The areas must then be ranked according to conservation priority. Finally the human/cat conflict in the priority areas must be identified and mitigation measures tested and implemented.

As discussed earlier, mammalian carnivores are frequently the "perfect" umbrella species: occupying the top of the food chain, their survival is linked to the survival of a complex ecosystem. Jaguars and pumas cannot be considered umbrella species for primary tropical forests since they can survive in disturbed habitat and might even survive better in such habitat.

There is no evidence that jaguars are keystone species and do not play a fundamental role in the maintenance of a certain habitat type. There was no significant difference between the species composition of prey species on Barro Colorado Island (which no longer supports large cats) and the mainland prey species in Panama (Wright et al. 1994).

Conservation organisations often use jaguars and pumas as their flagship species. Their charismatic allure, rather than any biological or ecological function, attracts attention. Jaguars are an important flagship species in Belize, here no tourist brochure is without a photo of a jaguar to portray forest wilderness. The official government magazine for tourist industry contained advertisements of 22 large inland tourist loges, 19 of these had a jaguar in the advertisement brochure (Destination Belize, edited and printed by the Belize Tourism Board, distributed among local tourist establishments, no overall editor mentioned).

The conservation community must be realistic. It is not possible to conserve every jaguar and puma population but the focus of conservation efforts should be data driven. This requires reliable abundance estimates from the different regions of their range combined with information on the perceived threats in the region.

There is a great need for a reliable standardised methodology to estimate abundance of jaguars and pumas across their range. Accurate scientific data is vital to shape policy. Chapters 2, 3 and 4 investigate a novel method of estimating jaguar abundance using camera traps.

# Available ecological knowledge on jaguars and pumas

Conservation policy requires ecological knowledge of the target species. It is useful to examine data from other species with similar ecological requirements for comparison. In this section the available data on the behavioural ecology of the jaguar and puma are presented and compared with other large cat species, highlighting any gaps in current knowledge.

In popular natural history reading the five Panthera species and the closely related puma and cheetah are defined as "big cats" (for example "Cats" edited by Seidensticker & Lumpkin 1991). This is based on size rather than phylogeny (Table 1.1, for more detailed information on phylogeny of jaguars and pumas see Appendix A). The jaguar has a similar length/mass ratio as lions and tigers. It has a stocky build with relatively short legs and tail. In contrast the puma has a very high length/mass ratio. It is slender with relatively long legs and a long tail. These morphological differences may facilitate co-existence of the two cats (Chapter 6).

Table 1.1 The seven largest cat species: mean body mass and range of head-body length of males (Nowell & Jackson 1996).

| | Average body weight (kg) | Head body length (cm) |
|---|---|---|
| tiger | 203 | 220-280 |
| lion | 200 | 200-280 |
| jaguar | 94 | 100-180 |
| leopard | 64 | 95-190 |
| puma | 58 | 105-200 |
| snow leopard | 58 | 100-130 |
| cheetah | 49 | 120-150 |

## *Current range of jaguars and pumas*

During the Pleistocene ancestral jaguars ranged from Europe to western Asia however competition with lions, tigers and leopards must have caused their extinction in these areas (Hemmer et al. 2001). Their geographic range has greatly contracted over the past 100 years; today they exist only in the neotropics (South and Central America, see Figure 1.1).

Figure 1.1 Geographic distribution of the jaguar: at the start of the 20th century (red) and the start of the 21st century (green, from Sanderson et al. 2002).

The puma has the largest geographic distribution of all cat species in the Americas and the longest north-south range of all cats in the world (see Figure1.2). Physical differences between jaguars from different regions are minimal and the main difference is in body size. Puma body size varies greatly along their north-south range; larger individuals are found with increasing distance from the equator, following Bergmann's Rule (Mayr 1963, Iriate et al. 1990, Gay & Best 1996). Jaguar body size seems to vary with habitat, the largest jaguars occur in flood plain areas of the Llanos in Venezuela and the Pantanal in Southern Brazil whilst the smallest jaguars inhabit the dense forest areas of Central America and Amazonia (see Table 1.2). It has been proposed that large body size is associated with the availability of high numbers of larger prey animals in the flood plain areas compared to the forest areas (Hoogesteijn & Mondolfi 1996).

Table 1.2 Mean body mass and skull length of male and female jaguars from flood plains and forests near and far from the equator (from Hoogesteijn & Mondolfi 1996).

| | Distance from | Bodyweight (kg) | | skull length (mm) | |
|---|---|---|---|---|---|
| Habitat type | Equator | Males (N) | Females (N) | Males (N) | Females (N) |
| Floodplains | Close | 104.5 (26) | 66.9 (31) | 289.6 (23) | 242.8 (23) |
| Floodplains | Far | 99.5 (24) | 76.7 (18) | 290.5 (48) | 257.6 (28) |
| Forest | Close | 83.6 ( 9) | - | 262.6 (19) | 237.0 ( 4) |
| Forest | Far | 56.1 (12) | 41.4 ( 8) | 243.6 ( 7) | 215.2 ( 4) |

Figure 1.2 Geographic range of the puma (green, from Nowell & Jackson 1996).

No data are available on the relationship between size of jaguars and pumas in the same area. Variation in size may be expected if they occupy different food niches. Jaguars are generally heavier and are expected to take the larger prey species. Chapter 8 investigates differences in feeding habits between the two cats.

## *Habitat plasticity of jaguar and the puma*

Jaguars occupy a variety of habitats, although they are often associated with water (Nowell & Jackson 1996; Kitchener 1991). Unlike many other cats they spend much time in the water and swim well and can survive in deserts, as long as there is a stream with some gallery forest as cover (Kitchener 1991). Today they do not occur in open savannah areas, although they used to inhabit the Argentinean pampas and the savannahs of southern Venezuela prior to European settlement on the continent (Hoogesteijn & Mondolfi 1996). Vulnerability to human persecution on these exposed lands probably contributed to their extirpation from these areas. Jaguars are also thought to be intolerant to cold (Hoogesteijn & Mondolfi 1996), therefore their range does not extend into high elevation areas and historically their range did not extend as far north or south as the puma. The present day habitat of the jaguar is characterised by areas with a relatively high temperature, vegetation cover and water.

Pumas currently occupy a higher variety of habitats than the jaguar, in contrast to the jaguar they are far more tolerant to cold conditions and they do live at higher elevation (hence their common name "mountain lion", Nowell & Jackson 1996). They also inhabit open environments such as the Argentinean pampas (where the jaguar is now extinct) and the Cerrado areas of Brazil (where the jaguar is rare).

## *Differences in reproductive output between jaguars and pumas*

Oestrus is relatively short in cats, ranging from 1.5 to 14 days with an average of 7 days for jaguars, coinciding with dispersal of young (Table 1.3, Kitchener 1991). This leaves a brief window of opportunity for mating. Females must advertise their reproductive state and males must respond to these signals. More than one male can react to the female's advertisement, for example in both tigers and pumas multiple males will pursue a single female in oestrus (Schaller 1967; Seidensticker et al. 1973).

Gestation periods of jaguars and pumas are similar however pumas produce larger litters and the off-spring disperse sooner (Table 1.3). This gives pumas a potential breeding advantage compared to the jaguar. Rearing cubs is a considerable burden on the energy budget of a large cat. First she must lactate and then after weaning she must catch enough prey to feed herself and the cubs. This period is shorter for pumas than for jaguars. The higher breeding output of pumas could potentially give pumas an edge when competition is high between the two species. In Chapter 6 the potential mechanisms of coexistence between jaguars and pumas are explored.

Table 1.3 Reproductive data on of jaguars and pumas (Kitchener 1991, Nowell & Jackson 1996).

| | **Jaguar** | **Puma** |
|---|---|---|
| Gestation in captivity (days) | 91-101 | 89-98 |
| Mean litter size (range) | 2 (1-4) | 3 (1-5) |
| Weight at birth (g) | 800 | 400 |
| Age at dispersal months | 18-24 | 12-18 |

## *Evidence of infanticide in cats*

Infanticide by male cats has been documented in lions (Bertram 1978; Packer & Pusey 1988), tigers (Schaller 1967), ocelots (Emmons 1988), pumas (Hornocker 1970) and Canadian lynx (Quinn & Parker 1987 in Kitchener 1991). This lowers the reproductive success of rival males and increases their own reproductive success by stimulating oestrus in the female. Infanticide has not yet been described in jaguars but is likely to occur. Such behaviour could encourage females with cubs to avoid males, especially in areas where males have unstable home ranges. Active avoidance of males by females could make it difficult to estimate abundance, if a subset of the population is effectively trap shy because they avoid the high traffic sampling locations. Differences in catchability between the sexes are explored in Chapter 5.

## *Social structures and spatial distribution patterns of large cats*

There are few data on the social structure of jaguars. Most natural history accounts classify them as solitary animals that only meet during mating and the males play no role in rearing the young (Nowell & Jackson 1996; Kitchener 1991; Emmons 1991). This is mostly based on scanty observational data and extrapolations from similar species like leopards (*Panthera pardus*) and tigers for which more data are available. On the basis of evolutionary theoretical models, the spacing of males and females is related to their role as caretakers of the offspring (Clutton-Brock 1989). It is widely accepted that the caretaker sex, frequently the female, will disperse according to resources (e.g. food, den sites) and predation threat, while males will distribute themselves in such a way so as to mate with the maximum number of females (Davies 1991). This model of females distributing themselves according to resources and males according to females has been demonstrated experimentally with voles (Ims 1988). This pattern is observed in the leopard and the tiger and is discussed below.

Female tigers and leopards maintain exclusive territories to other females, defending home ranges with defined boundaries that have enough food for themselves and their offspring (Sunquist 1981; Mizutani & Jewell 1998). Home range size of female tigers is positively related to prey density (Miquelle et al. 1999; Sunquist et al. 1999), with larger male home ranges surrounding several female ranges (Figure 1.3).

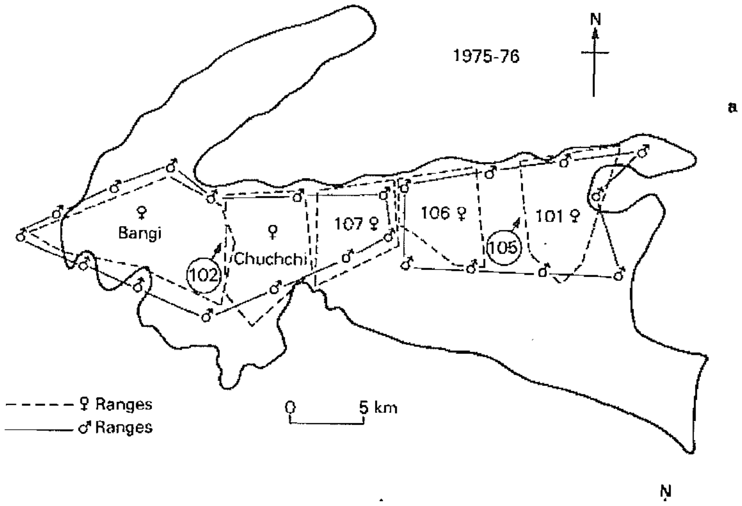


Figure 1.3a. Configuration of tiger territories (male and female) in Chitawan National park, Nepal. From Sunquist (1981).

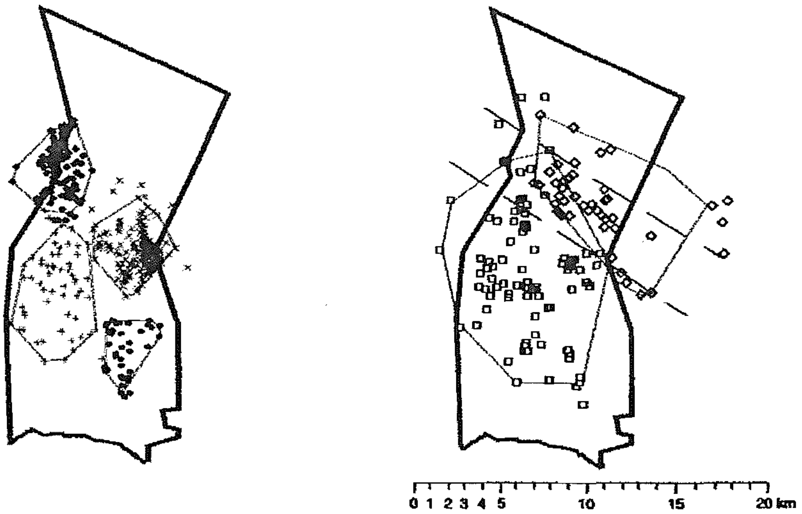


Figure 1.3b. Configuration of leopard territories in Laikipia game district, Kenya. From Mizutani & Jewell (1998). Female territories are shown on the left. Male territories are shown on the right. Both depict the same area.

This system results in a few males having access to relatively many females. Only dominant males can maintain exclusive territories, subdominant males either live at the margins or within territories of others where they remain elusive. Subdominant males are sometimes tolerated as long as they do not attempt to mate. Dominant males have to be physically strong enough to drive off intruders and defend their large territory. This intense male-male competition manifests itself as a shorter reproductive lifespan of males compared to females. This was found for tigers in Chitawan National Park in Nepal and represents the only data of this kind available for solitary big cats (Smith & McDougall 1991). Male tigers maintained reproductive dominance for ~ 2.8 years (7months to 6 years) whilst the female reproductive lifespan was on average 6.1 years (maximum 12.5 years, Smith & McDougall 1991).

Exclusive home ranges of males and females separately are not the only system found in larger cats. In the Mount Hamilton area of the Diablo Range of California, male home ranges of pumas overlap extensively whereas females have exclusive home ranges (Hopkins et al. 1986). No potential explanation was given for this. In contrast, home ranges of female pumas in the Idaho Primitive Area overlap extensively, whereas male home ranges are exclusive (Seidensticker et al. 1973). The authors suggest that the high mobility of the prey, mainly deer, and the limited availability of hunting sites encourage the females to live and hunt in close proximity to each other. Kin relations between female cats using one home range may also explain overlap between the females. Females settle closer to their natal area than do males and sometimes stay within the home range of their mother (Seidensticker et al. 1973). This difference in dispersal pattern has been reported in leopards, lions and tigers (Nowell & Jackson 1996; Kitchener 1991). In Chitawan, McDougall (in Schaller & Crawshaw 1980) reported that female ranges may overlap extensively through time except in areas with low prey density; these were mostly related tigresses (mothers and daughters). Later work in the same area by Sunquist (1981) demonstrated the existence of exclusive territoriality in female tigers (Figure 1.3a).

Home ranges can also vary seasonally with prey migration. Pumas in Idaho expand and contract their home ranges as a reaction to prey movements throughout the seasons (Seidensticker et al. 1973). Ranges of leopards in Wilpattu National Park, Sri Lanka overlap during the dry season in converging on the a few waterholes remaining which attract congregations of prey species (Muckenhirn & Eisenberg 1973).

Telemetry studies usually provide detailed information about a few individuals. However overlap of home ranges can only be investigated for those individuals that are collared. No information is available on the movements of un-collared conspecifics also living in the study area. In this study, Chapter 5 discusses how camera trapping can provide range behaviour for many of the individuals inhabiting the study area, however monitoring is restricted to a limited number of locations.

## *Social structures and spatial distribution patterns for jaguars*

Few data on social structure of jaguars are available, as compared to leopards, tigers and lions. Six telemetry studies of jaguars can be compared. Male home ranges are generally larger than those of females; and jaguars inhabiting floodplain areas of the Venezuelan Llanos and the Pantanal have larger home ranges than those inhabiting the jungles of Central America (Table 1.4).

Table 1.4. Home range (Minimum Convex Polygon) of male and female jaguars in different areas based on telemetry.

| | | **Home range (km²)** | | |
|---|---|---|---|---|
| **Area of study** | **Country** | **Male** | **Female** | **Data source** |
| Cockscomb | Belize | 28-40 | - | Rabinowitz & Nottingham 1986 |
| Pantanal | Brasil | - | 25-38 | Schaller &Crawshaw 1980 |
| Pantanal | Brasil | 79 | 51-70 | Crawshaw & Quigley 1991 |
| Calakmul | Mexico | 32-59 | 33-41 | Ceballos et al 2002 |
| Jalisco | Mexico | 60 | - | Núñez et al 2002 |
| Llanos | Venezuela | 130 | 48-50 | Scognamillo et al 2002 |

### Females

In the floodplains of the Brazilian Pantanal and the Llanos areas of Venezuela, unrelated adult female jaguars maintain distinct home ranges with relatively low overlap (~30%, Schaller & Crawshaw 1980, Crawshaw & Quigley 1991, Scognamillo et al. 2002; Scognamillo et al. 2003, see Figure 1.4, range 3 and 11 and Figure 1.5). Núñez et al. (2002) reported extensive range overlap in the dry forest of Jalisco in Mexico for female-female, male-male and female-male ranges. All ranges were concentrated around the few sources of water in this dry area. Although they utilised the same space, the jaguars avoided each other in time - the mean distance between individuals was 4 km when fixes were taken simultaneously.

Broad overlap was noted between the ranges of mothers and sub-adult daughters in the Pantanal (Schaller & Crawshaw 1980, Crawshaw & Quigley 1991, see Figure 1.4: 11 = mother and 9 = daughter; 3 = mother and 1 = daughter). The sub-adult son dispersed much further such that there was no overlap (see Figure 1.4: 3 =

mother and 4 = son). Despite overlapping in space the mothers and daughters appeared to avoid each other in time. Only 1.3% of the simultaneous fixes found females closer than 1 km, 17.3% indicated that the distance between females was 1-5 km, 33.7% were 5-10 km and 48% were > 10 km apart (Crawshaw & Quigley 1991).

## Males

The ranges of adult males are larger than those of females and males show extensive overlap with several females (Schaller & Crawshaw 1980, Scognamillo et al. 2002, Figure 1.5). Extensive overlap was noted between 5 radio-collared males in the lowland broadlfeaf forests of Belize (Rabinowitz & Nottingham 1986, see Figure 1.6). However no fixes were recorded of two males being "close" together at any time (no additional distance data is given). Rabinowitz & Nottingham (1986) attribute this to the extensive system of logging roads which functioned as main travel routes. Clear paths are a limited resource in the dense vegetation of the Belizean jungle and this could account for the overlap. The males would concentrate their activity in small areas (as small as 2.5 km$^2$) for up to a week (range 4-14 days) before shifting, in a single night, to another part of their range.

Even though there was much overlap of the males' ranges in Belize and they avoided each other in time, it is likely that there was also spatial avoidance: following the deaths of two males, two other male jaguars expanded their ranges into the ranges of previous owners suggesting that spatial avoidance exists independent of time (see Figure 1.7). Spatial avoidance between jaguars is further explored in Chapter 5.

## Seasonal variation

Seasonal variation in jaguar home range was reported in the floodplain areas of the Venezuelan Llanos, Brazilian Pantanal and the dry seasonal forest of Jalisco, Mexico. Home range size varied in the floodplain areas, contracting dramatically during the wet season and expanding in the dry season (Crawshaw & Quigley 1991; Scognamillo et al. 2003). The reverse pattern was observed in Jalisco (Núñez et al. 2002), here the home range size, only available for females, was smaller in the dry season (25 km$^2$) than in the wet season (60 km$^2$). These variations can be explained in terms of prey movement. During the wet season in the flood plains the prey move to the few areas of dry land, restricting the range of jaguars, then spread out again over the plains during dry season. In the dry forests of Jalisco the prey concentrate around the few remaining water sources during the dry season and scatter during the rainy season when more water is available in dispersed locations.

## General conclusions about jaguar spatial patterns

Jaguars are solitary, but their spatial distribution patterns vary across their range. Seasonal congregation and movement of prey, habitat differences and density of jaguars are likely to contribute to this variation. It is difficult to draw conclusions about the social system because most of the studies to date have either focused on males or on females and adolescent males. Commonly there is broad spatial overlap combined with temporal avoidance. Scognamillo et al. (2002) and Schaller & Crawshaw (1980) were the only studies to find evidence of the "classic" cat social system (one male overlaps multiple females, see Figure 1.5).

Information on spatial distribution of target species is necessary to plan any study of abundance estimates. For example, configuration and spacing of camera trap locations has to be based on known spatial patterns of the target species. If this is not available it should be based on other related cat species or from other areas (see Chapter 2). This present study was conducted in the same area where Rabinowitz & Nottingham (1986) studied jaguars and so the configuration of traps for abundance estimates in Chapter 2, 3 and 4 are based on their estimates of jaguar home range.

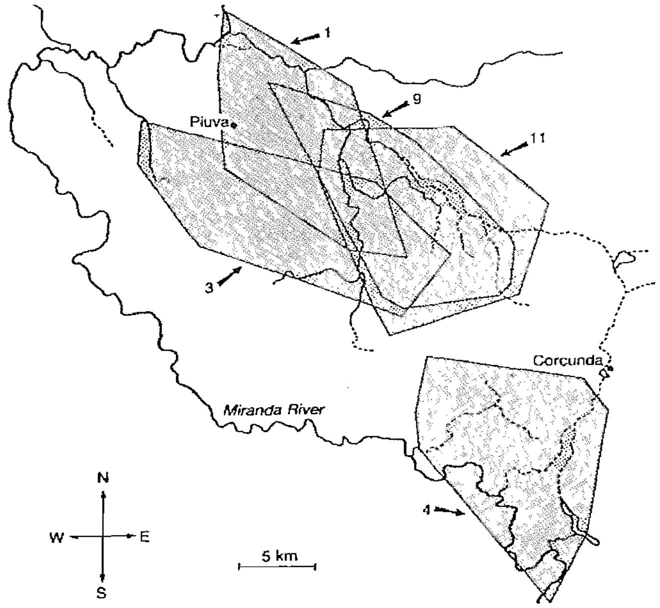


Figure 1.4. Home ranges of five jaguars, four females and one male in the Pantanal, Brazil. From Crawshaw & Quigley (1991).

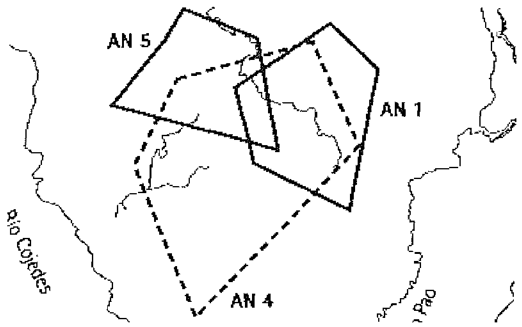


Figure 1.5. Home ranges of three jaguars, two females and one male in the Llanos area, Venezuela. From Scognamillo et al. (2002).

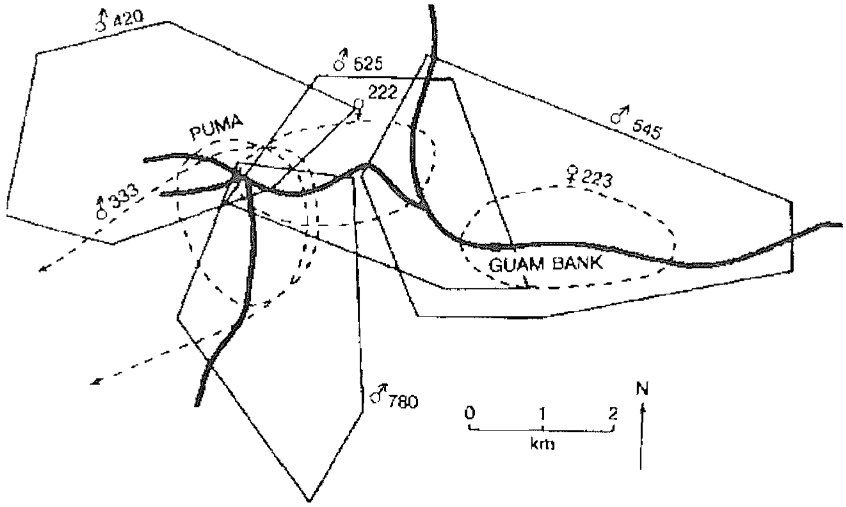


Figure 1.6. The home ranges of four males in the Cockscomb Basin, Belize (solid lines). Ranges of females and pumas (dashed lines) were estimated using track data. From Rabinowitz & Nottingham (1986).

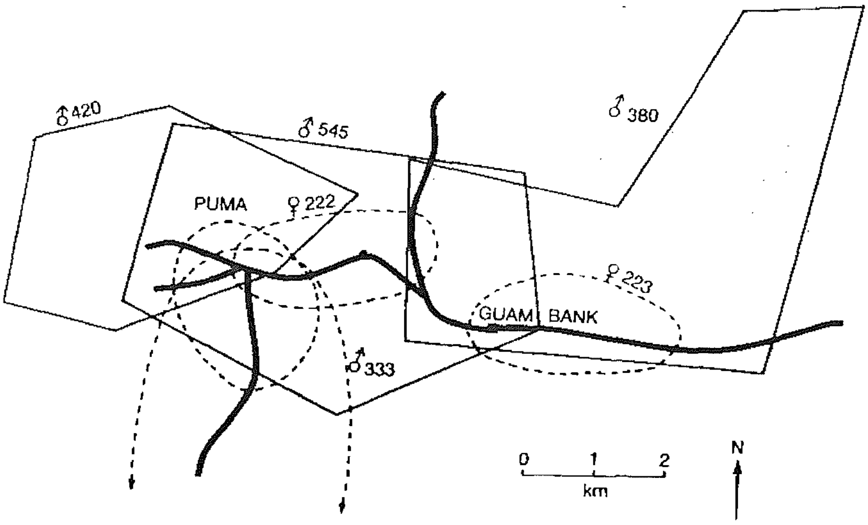


Figure 1.7. The shifting home ranges a year later of three males (solid lines), see Figure 1.6 after two of the males died. Ranges of females and pumas (dashed lines) were estimated using track data. From Rabinowitz & Nottingham (1986).

## *Communication between cats*

Most cat species are rather solitary yet they still have to communicate with each other. Vocalisation and olfaction as methods of communication between cats are discussed in this section. Olfaction is described in more detail since this is the main system of long-term communication between cats (Kitchener 1991).

## Vocalisation

Vocal communication is used by cats but few systematic data are available from the wild. All *Panthera* species can roar. Both male and female jaguars give a "sawing" call, often associated with mating (Emmons 1991). Schaller & Crawshaw (1980) noted that vocalisations were not heard in their study area in the Pantanal, whilst Miller (1918, in Schaller & Crawshaw 1980) heard jaguar calls every night in the Orinoco delta of Venezuela. Emmons (1987) reported that roaring was rare and mostly involved bouts of calls and counter-calls from a nearby conspecific. Rabinowitz & Nottingham (1986) did not report on any vocalisation in Belize, but Rabinowitz (1986) discusses the use of "jaguar callers", used by Belizean hunters to imitate jaguars and attract them to an area. Such callers have been widely used throughout their range to successfully attract jaguars. This suggests that vocalisation plays an important role in jaguar communication. It may function in territory defence or the attraction of mates. During this study sporadic vocalisations were heard, mainly during the wet season.

No data are available on vocalisation patterns of pumas. The call of pumas is akin to that of a domestic cat but somewhat louder (pers. obs. B. J. Harmsen, thesis author).

## The use of olfaction

Cats have a relatively poorly developed sense of smell compared to other Carnivores. Canids, mustelids and ursids all depend on olfaction to detect food whilst cats use olfaction for communication rather than hunting. Brain volume dedicated to olfaction and surface area in the nasal cavity are smaller in felids compared to canids, although cats have more types of receptors in the nasal cavity compared to dogs (Kitchener 1991). Cats can produce scent from glands on four regions of their body: the face, the anus, above the tail and between the toes (Kitchener 1991).

## Scent marking: to defend a territory

Cats leave olfactory marks when walking through their territory. Spraying urine is the most common method (Smith et al. 1989). Male cats have a retractable penis that allows them to direct urine on to vertical objects (for example trees) at a height that can be easily detected by conspecifics. Table 1.5 shows large variation in marking frequency of several species of cats, indicating that males tend to scent-mark more frequently than females. Other means of marking include: faeces (scats), scrapes along the ground, scratches on tree trunks, and flattening vegetation by rolling on the ground.

Table 1.5 Urine spray frequency of four species of felid.

| | | Sprays per km | | | |
|---|---|---|---|---|---|
| **Species** | **Scientific name** | **Males** | **Females** | **Unknown** | **Source** |
| Serval | *Felis serval* | 41.2 | 15 | - | Kitchner 1991 |
| Bobcats | *Lynx rufus* | - | - | 1.9 - 7.5 | Bailey 1974 |
| Canadian lynx | *Lynx canadensis* | - | - | 10.6 - 12.5 | Sanders 1963 |
| tigers | *Panthera tigris* | 2.4 | 1.8 | - | Smith et al. 1989 |

Urine is often sprayed on the underside of leaning trees to protect it against rain and in visually distinct places (Smith et al. 1989). Visual aspects of the marking play an important role (Smith et al. 1989). Cats may urinate on the ground and scrape their hind feet through the patch of urine. Pumas commonly scrape together a pile of dead leaves and then urinate on it (Seidensticker et al. 1973). Defecating in scrapes was recorded for tigers (Smith et al. 1989). Tigers only scraped in open areas where spray marking was not possible. Multiple deposit sites of faeces (latrines) have been recorded for ocelots (*Leopardus pardalis*), bobcats and wildcats (*Felis silvestris*, Kitchener 1991).

Urine and faeces have to be regularly replaced to reinforce their signal. Faeces and especially urine loose their olfactory function rapidly through time. Male domestic cats can distinguish new from older urine markers (de Boer 1977). This suggests that the scent-marks may signal how recently the owner was in the area. Cats may be able to deduce information such as proximity (based on decay rate), sex, sexual status and potentially health. If so, such signals could reduce the level of aggressive encounters by giving accurate information to intruders and residents about the status of conspecifics.

Corbett (in Kitchener 1991) noted a “marking war” in Scottish wildcats when an intruder started marking inside the territory of a resident. The marking frequency of the resident increased tenfold and the resident marked over every urine spray left by the intruder. The only study that considers scent-marking in relation to territory maintenance is of the tigers in Chitawan by Smith et al. (1989). The distribution of territories was similar to that in Figure 1.3a. Visiting rates of all the areas within a home range were similar but spraying rate of males and females increased at the border areas. When a neighbouring female marked boundary areas, the resident female doubled her marking effort in this region. Contact zones of two territories on well-travelled routes tended to have high concentration of markers in the contact zone. This was found for both male and female tigers. High rates of scent-marking were also noted when home ranges were established by dispersing males and females. The rate of marking decreased once the range was established. These data suggest that scent-marking in cats has a territorial role.

There are few data available about marking behaviour in jaguars and pumas. Rabinowitz & Nottingham (1986) in their study in Belize noted that jaguar faeces were found in scrapes on road stretches that marked the overlap zones between male jaguar home ranges. The number of scrapes found in this study was low ($N = 40$). 68% of the scrapes contained faeces but urine was never detected in scrapes. Only a few (unreported percentage) scrapes were found that were assigned to pumas (presumably based on tracks), half of these contained urine and none contained faeces. 70% of the jaguar scrapes were recorded in 7 days when two adult male jaguars were known to have walked the same road. No other types of marking, such as urine spraying, were reported. This is in contrast to Seidensticker et al. (1973), who found scraping a common way of marking by pumas. Few markings were noted in the Brazilian Pantanal and the few scrapes found were assigned to pumas (Schaller & Crawshaw 1980, Crawshaw & Quigley 1991). Emmons (1987) reported that in Peru jaguars of both sexes scrape intensely every few 100m, and urine or faeces were always found in these scrapes. Jaguar scraping was noted at spatially and temporally irregular intervals, while puma scraping was much more regular and frequent. Both jaguars and pumas were noted to scratch trees in the area. No overall patterns or functions have been proposed for jaguar or puma marking.

Scrape marking of jaguars and pumas is investigated in Chapter 9. A long-term study of scrapes was carried out in combination with camera trap data and several hypotheses of the function of scrapes are tested for both species.

### Scent marking: to attract a mate

Urine markings can convey the sexual status of females. For example, Molteno et al. (1998) found that scent-marking by black-footed cats (*Felis nigripes*) increased 6 weeks before mating. Black-footed cats are in heat for periods of only 36 hours and so mating opportunity is restricted to one night. Announcing this is of crucial importance for a strictly solitary species, to make sure that a mate is present. For the rest of the year the marking behaviour seemed to have the classic territorial function, and during periods when the black-footed cat had kittens she would rarely mark and instead buried urine or faeces around the den sites to avoid attracting predators. A similar increase in scent-marking was noted for tigresses in Chitawan (Smith et al. 1989). Here females doubled the rate of urine spraying a few days before oestrus but did not scent mark during oestrus. Male tigers increased marking fourfold when a female was in oestrus and visited the area twice as often. This behaviour is also observed in domestic cats (Kitchener 1991). Both male and female domestic cats use scent marking to advertise their presence to each other.

No data are available on marking behaviour of jaguars during the breeding season. It is likely that jaguars, like the two other cat species discussed here, use marks to signal their reproductive status. The potential for scent-marking to attract a mate is discussed in Chapter 9.

## *Evidence for interspecific competition*

So far the natural history and ecology of jaguars have been discussed in isolation independently from pumas. However the puma is a similar size to the jaguar and overlaps with its entire range potentially giving rise to competition between the species.

### General mechanisms of interspecific competition

Inter-specific competition occurs wherever there is a limited resource, often food but other resources may also be limited, for example den sites. Scramble competition describes the situation where both species utilise the same resource but avoid direct confrontations. In contrast interference competition describes the situation where the dominant species actively pursues and kills the other species, for example lions actively try to kill cheetahs (*Acinonyx jubatus*, Durant 1998). Such competition could drive cheetahs to extinction unless they can avoid it. Simple Lotka Volterra models predict that the carrying capacity of both species is reduced when two similar species compete for the same resource when interspecific competition is low between the two species. High levels of interspecific competition will cause unstable equilibrium points and the eventual extinction of inferior competitor (Begon et al. 1996; Tokeshi 1999). The high number of species coexisting sympatrically, competing for the similar resources, suggests that there must be mechanisms that allow coexistence, avoiding high levels of competition.

## Coexistence between carnivores

The following mechanisms of co-existence have been described for sympatric carnivores:

1) Different prey species or size classes: In Nagarahole National Park in Southern India tigers were found to concentrate on larger prey whilst leopards and dholes (*Cuon alpinus*) took medium sized prey. Leopards and dholes selected different types of prey species: dholes concentrated on male axis deer (*Axis axis*) and wild pigs (*Sus scrofa*) and leopards hunted a wider variety of medium size mammals (Karanth & Sunquist 1995; Karanth & Sunquist 2000). In Sri Lanka, where there are no tigers or dholes, leopards are known to take larger prey (Muckenhirn & Eisenberg 1973). A similar relation between tigers and leopards was observed in Chitawan National Park in Nepal (Seidensticker 1976) and for lions and leopards in the Serengeti, Tanzania (Bertram 1982).

2) Different activity patterns: Karanth & Sunquist (2000) reported that dhole and leopard hunt during different times of the day. Fedriana et al. (1999) reported that red foxes (*Vulpus vulpus*) and Iberian lynx (*Lynx pardinus*) hunt during different times of the day for rabbits, with the lynx mainly hunting at dusk and dawn and the fox through the night. Lynxes are the dominant predator and are known to kill foxes if given the opportunity.

3) Different habitat use within the area: Fedriana et al. (1999) reported that lynx mainly hunt in shrub land where rabbit populations are high whilst foxes mainly hunt on pasture land that is comparatively low in rabbits. If the lynxes were not present foxes might use the shrub land more often for hunting and subsequently their numbers

would increase. Habitat separation was also reported in Chitawan, Nepal where tigers mainly hunt the grassland and leopards mainly hunt in the forested areas (Seidensticker 1976).

4) Differential use of space: Durant (1998) reports that in the Serengeti in Tanzania (where there is a high density of lions and hyaenas) cheetahs hunt mainly in areas with medium to low abundance of their preferred prey, Thompson gazelle (*Gazella thomsoni*), while lions and hyaenas hunt only in areas with high or medium abundance of Thompson gazelle. The habitat in these areas is similar, suggesting that habitat features are not responsible for this spatial separation of cheetahs from lions and hyaenas. They may be actively avoiding lions and hyaenas, but they are also better adapted to hunt low prey densities, which are less vigilant against solitary hunters than larger herds. Cheetahs are able to co-exist with the lions and hyaenas of the Serengeti by utilizing the areas with lower prey densities. Fedriana et al. (1999) reported that lynx and badgers (*Meles meles*) in Spain have different strategies for hunting rabbits and utilise the space differently. Badgers mainly dig young rabbits out of their burrows while lynx hunt adult rabbits that are foraging.

These four mechanisms allow carnivore species to coexist in the same area. In such cases competition of the past may have resulted in coexistence between two species in the same area (Begon et al. 1996; Tokeshi 1999). Human disturbance can disrupt the equilibriums of these complex systems that have been fine-tuned over millennia. Segregation between carnivores based on prey size can be disrupted when humans start competing with the predators and reduce populations of large herbivore prey species. National Parks in Africa often encourage mega fauna for eco-tourism. These areas have high densities of lions and hyaenas. Land that is less rich in wildlife is converted to agriculture and lethal control of predators turn them into ecological sinks. These areas with lower densities of prey are the most suitable areas for cheetahs and they are rapidly disappearing. Rabinowitz & Walker (1991) reported that the leopard density was higher than tigers in the Huai Kha Khaeng Wildlife Sanctuary in Thailand yet leopards usually live at lower densities when another dominant predator is present. Poaching had disturbed the prey assembly and reduced most of the larger deer and bovine species to unnaturally low densities. The tigers had to resort to hunting mainly small deer such as muntjac. The leopard is smaller and so better adapted to take muntjac prey than tigers. Human impact on habitat or prey species can therefore greatly influence the competitive balance between two predator species and shift the roles of dominance in a relatively short time. Consequently it is important to understand the nature of coexistence between two potentially competing species so that the potential impact of human interference can be predicted.

## Coexistence between jaguars and pumas

The puma is the only significant competitor of the jaguar. The smaller neotropical cats, the ocelot, margay (*Leopardus wiedii*), jaguarundi (*Herpailurus yaguarondi*) and oncilla (*Felis tigrina*) are much smaller and are classified as prey species rather than as competitors, as are the mustelids, canids and procyons (raccoon Family) that live within the jaguar's range.

It is likely that the jaguar would win in direct conflict with the puma. On average the jaguar is heavier and more powerfully built than the puma but there is much overlap with large male pumas being much larger than small female jaguars. There is some evidence of jaguars killing pumas and even of a jaguar eating a puma (Crawshaw & Quigley 2002; pers. comm. B. Miller, consultant jaguar research, Wildlife Conservation Society). In this respect the competition would have a neutral effect on the jaguar and a negative effect on the puma. The main negative effect for jaguars from pumas would be in the exploitation of the same prey base. Before discussing hunting and prey species of the two cats, the available data on spatial and temporal segregation will be discussed.

Schaller & Crawshaw (1980) found no difference in habitat use between puma and jaguar in their study area in the Pantanal, Brazil. They noted that pumas tended to avoid certain valleys that were often visited by jaguars (no quantitative data are given). They also reported that pumas tended to frequent the drier Cerrado habitats in the Pantanal whilst the jaguars preferred wetter habitats. They did not study temporal segregation.

Rabinowitz & Nottingham (1986) observed tracks of jaguar and puma throughout their study area in Belize. Pumas and jaguars used similar paths on many occasions. Local knowledge indicated that puma are rare in areas where jaguars are abundant. This has not been supported by scientific study.

Núñez et al. (2002) found in the dry forests of Mexico that the density of puma was 3.5/100 km$^2$ compared to 1.7 jaguars/100 km$^2$. They did not find any significant difference in habitat use or activity patterns between jaguar and puma. Both species preferred the areas around the few water systems available. It could be that pumas are better at utilising the drier areas away from the waterways compared to the jaguars, explaining their higher density. Mean distance between jaguars and pumas when simultaneous fixes were taken were not significantly different from mean distance between jaguars (~4 km). They also reported that jaguar and puma marked close to each other.

Emmons (1987) reported some habitat segregation between jaguars and pumas in Peru. Jaguar tracks were frequently found along the river and beach areas of lakes and they were often sighted walking or sunning along rivers. In contrast pumas or their tracks were rarely seen in these areas. Tracks of both species were found within the forest and the trails were used by both species.

Scognamillo et al. (2003) reported overlap of 50% to 60% in home range between jaguars and pumas in Venezuela. Pumas were more active than jaguars but there was no significant difference in timing of activity. Both cats occupied different habitat types in similar proportions indicating no differential use of habitat. There was little simultaneous overlap between the location of jaguars and pumas suggesting active avoidance. The complex variety of the landscape was proposed as a potential mechanism for this avoidance since habitat and activity differences were minimal.

Potential mechanisms of coexistence between jaguars and pumas will be presented in Chapter 6 and 8. Chapter 6 investigates spatial and temporal avoidance between the two species and Chapter 8 investigates dietary separation.

## Hunting

Jaguars and pumas have the potential for a 100% dietary overlap. The lack of spatio-temporal separation observed between jaguars and pumas suggests that a dietary separation may be the mechanism of their co-existence. Jaguars and pumas both climb well and can be found resting in trees. They rarely seem to hunt above the ground. There are instances of primates being taken, suggesting that they either surprise them on the ground or in their sleep at night (Peetz et al. 1992). Kiltie (1984) compared several morphological features of the five neotropical cats and found that relative gape differed significantly between the species. There was a linear relationship between relative gape and body mass. The gape size of a cat is considered to represent the upper limit of prey size that the predator can handle. This supposedly gave morphological evidence that the neotropical cats separate themselves by diet. Jaguars have the most powerful jaws of all cats. This allows them to kill with a nape bite, crushing the neck vertebrae or skull (Emmons 1991). Pumas have smaller heads and jaws and so mainly kill by suffocation. They close the windpipe of the victim by grabbing its throat. Pumas only use a nape bite on the smallest prey animals.

Most cats hunt by sight and hearing is used as a secondary sense (Kitchener 1991). Olfaction is thought not to be used for hunting (Kitchener 1991). When a prey animal is encountered, cats either "sit and wait" for the prey to come closer or they stalk the prey. The final chase consists of a few powerful jumps to overpower the prey and kill it (Kitchener 1991). Like all cats, jaguars and pumas are unable to maintain high speeds for a long time and thus unable to maintain a chase for long distances (Kitchener 1991). Almost all prey species have greater stamina than cats and can outrun them over longer distances. The distance at which the final chase can be made is a function of the acceleration of the cat and of the prey species. There are no data available for acceleration ability of either the puma or the jaguar. The lighter build of pumas, and longer legs, suggests that they can accelerate faster than jaguars, giving them a wider window of opportunity for the final chase. It is also likely that the lighter puma has greater stamina that the jaguar, and are perhaps more successful hunters than jaguars in open areas. Ability to chase prey might not be adaptive in areas of dense undergrowth. Here the heavy build of jaguars is likely to be better adapted than the puma for killing and quickly overpowering strong and large prey. These hypotheses are tested in Chapter 8 in terms of differences in diet and Chapter 6 in terms of frequency of walking "off-trail".

## Prey species

The prey assembly is similar throughout the entire range of the jaguar. Mega-fauna, as found in Africa, Asia and North America, are lacking in Latin America. There are no large group-living deer, horse or bovine species present in the range of the jaguar (except domestic animals). The largest species is the solitary tapir, which is significantly larger than the next heaviest animal. The deer species are small and generally solitary, especially in dense forest areas. The only large animals that live in groups are the peccaries. The next biggest group are the large rodents. Except for capybara (*Hydrochaeris hydrochaeris*), which are not present over the whole jaguar range, all these species weigh ≤10 kg and are mostly solitary. There are also a wide range of small rodents, carnivores, marsupials, larger reptiles, birds and fish potentially available. Availability of prey is further discussed in Chapter 7.

### Diet

It has been suggested that pumas eat smaller prey animals in areas where they compete with jaguars (Iriate et al. 1990). A detailed account of diet is presented in Chapter 8. Both jaguars and pumas take a wide variety of prey species over a large size range (Sunquist & Sunquist 2002). Both cats are noted to eat small rodents and lizards ≤1 kg but larger mammals comprise most of the cats' diet. There is great variation between different studies in the percentages of large prey eaten by these two cat species (Sunquist & Sunquist 2002). This is probably due to differences in availability of larger prey species in different regions. Low densities of large prey force them to switch to more abundant, smaller prey species. It can be concluded that both jaguars and pumas have similar ecological requirements in prey and habitat throughout their overlapping range. Local habitat conditions might give one a competitive edge over the other. Jaguar and puma competition and coexistence in light of diet are discussed in Chapter 8.

## Thesis objectives

Radio-telemetry studies of jaguars and pumas tend to require several years of high trapping effort, with a return of small samples of animals (*N* = 2 to 5, e.g. Schaller & Crawshaw 1980, Crawshaw & Quigley 1991, Rabinowitz & Nottingham 1986, Núñez et al. 2002, Scognamillo et al. 2002). Radio telemetry is a useful tool, but in the case of jaguars and pumas, it is time consuming, expensive and inefficient. In addition, the capture and anaesthetization of large felids is traumatizing for the individual, and may on occasions have fatal consequences arising from injuries sustained during trapping or irregularities with anaesthetisation (for example Rabinowitz 1986). Large felids are notoriously difficult to anesthetise safely (pers. comm. H. Quigley, Consultant jaguar research, Wildlife Conservation Society). This is unacceptable, especially when dealing with threatened or endangered species. This study focuses on the development and optimisation of non-invasive methods to study jaguars.

The most important information required to formulate conservation policy is the abundance of the target species. Conservation action can only be evaluated if the target population can be monitored. This requires a standardised method to count or to accurately estimate the number of individuals present in the area.

Prediction of future events is also important in formulating conservation policy: population stability and the likely effect of ecosystem changes on the population. The dynamics of the following key factors influencing abundance need to be understood:

1) Availability and access to food (survival rate)
2) Level of predation (survival rate)
3) Level of competition with other species for resources (survival rate)
4) Reproductive capacity (recruitment rate)

## *Development of accurate methods for abundance estimates*

Abundance and density estimates are necessary to develop conservation policy for large neotropical cats. This requires a reliable methodology that can be applied across the whole range of the jaguar and puma. The primary method investigated in this thesis is camera trapping. Chapter 2 explains the general methodology of camera trapping and the design of surveys using camera traps. Jaguars can be individually recognised by the pattern of rosettes on their pelt and this allows for accurate abundance estimates using mark-recapture analysis. Individual identification is not so easy for species like pumas which lack markings. Other, less accurate, methods of estimating abundance of pumas are investigated in Chapter 6. Chapter 2 describes the annual large-scale survey repeated every year (2002 to 2005) during the dry season (February to April). Jaguar abundance estimates are calculated from the data collected during these surveys using mark-recapture models. Annual variation in abundance estimates are discussed.

Effects of temporal and spatial variation in jaguar abundance estimates based on camera trap surveys are explored in Chapter 3 and Chapter 4. In Chapter 3 temporal and spatial variation is studied with the use of simulation studies and re-sampling of the original data. Simulations are used to explore the effects of catchability on abundance estimates by varying the catchability coefficient.

In Chapter 4, data are presented on camera trap surveys conducted in smaller areas with a higher density of cameras to study the effects of camera deployment on abundance estimates with special reference to optimal distance between cameras and micro-location (trail width, trail age, distance to water, altitude, slope). Comparisons are made between abundance estimates of the annual large-scale survey and these small-scale high camera density surveys. Seasonal variation in jaguar abundance estimates is also investigated in Chapter 4. Conclusions are drawn about the optimal survey design in terms of spatial distribution of cameras, length of survey and seasonal variation.

## *Ecological data on jaguars and pumas*

The available data on the behavioural ecology of jaguars and pumas have many gaps. Most of the data come from telemetry studies, which provide detailed information of the spatial and temporal movements of a few individuals. Camera trapping provides few data points for many different individuals. This could fill some of the gaps.

Chapter 5 explores the usefulness of camera trapping as a tool for answering ecological questions about jaguars. Although the surveys were not designed to study the social systems of jaguars, they provide a wealth of data of continuous capture histories of a large number of individuals. Temporal and spatial segregation between individuals are discussed and conclusions are drawn about range overlap and territorial behaviour. The use of open population models for the estimation of life-history parameters was tested for jaguars using the yearly repeated camera trap surveys.

Chapter 6 explores the usefulness of camera traps for estimating abundance of pumas. The jaguar and puma data are compared. If individual recognition of pumas is not possible, the comparison between the species will be done more broadly using sheer capture rate of the two species as the unit of analysis.

## Feeding habits of jaguars and pumas

The potential for competition between jaguars and pumas is clear from the information provided on feeding behaviour of the two cats. Potential competition between the two species in terms of food depends on the availability of food and the separation of these resources between the two species. Camera trap data can provide data on the availability of prey species in terms of capture records of the different prey species. This could be used as an index of relative abundance for the different prey species. Comparison with footprint surveys of prey show whether this index has any validity. Chapter 7 investigates the use of camera trap data to estimate relative prey and comparison were made between sign surveys and camera trap data.

Faeces (scats) of jaguars and pumas were collected for diet analysis to determine dietary overlap of the two cats. Chapter 8 describes a new method of distinguishing jaguar from puma scats, which remains in development. In the interim, diet analysis focuses on general trends between years and different areas using a uniquely large collection of large-felid scats. The data are compared with other areas and previous data from the same study area (Rabinowitz and Nottingham 1986).

## Marking behaviour of jaguars and pumas

Few data are available on marking behaviour of the neotropical cats. Signs of marking, if properly understood, can tell much about the structure of a population and could potentially be a useful tool for rapid surveys. In Chapter 9, marking behaviour of the large cats is investigated.

## Study Area

The main study area was within the Cockscomb Basin Wildlife Sanctuary (CBWS) in Belize (Figure 1.8). The CBWS was chosen as a study site because previous telemetry work has been done on jaguars in this area (Rabinowitz & Nottingham 1986), providing background information on behavioural ecology of jaguars in this area and the jaguar density was thought to be relatively high which is ideal for testing out new methodology (Silver et al. 2004). Furthermore the dense secondary forest is exactly the kind of habitat that requires a new non-invasive methodology.

The CBWS is a broadleaf tropical forest. The area was extensively logged 20 years ago and also used for traditional milpa farming by local Mayans. This has created a mosaic of secondary forest. The undergrowth is dense. Most forest in Belize is limestone based, like BNR. CBWS has a granite base, with fertile red clay soil in the flood plains. Several large permanent rivers flow through CBWS. Some of the smaller streams disappear during the peak of the dry season but most are permanent. The area has a dry season (Feb to June) and a wet season (June to March). For a more detailed description of the area see Rabinowitz & Nottingham (1986).

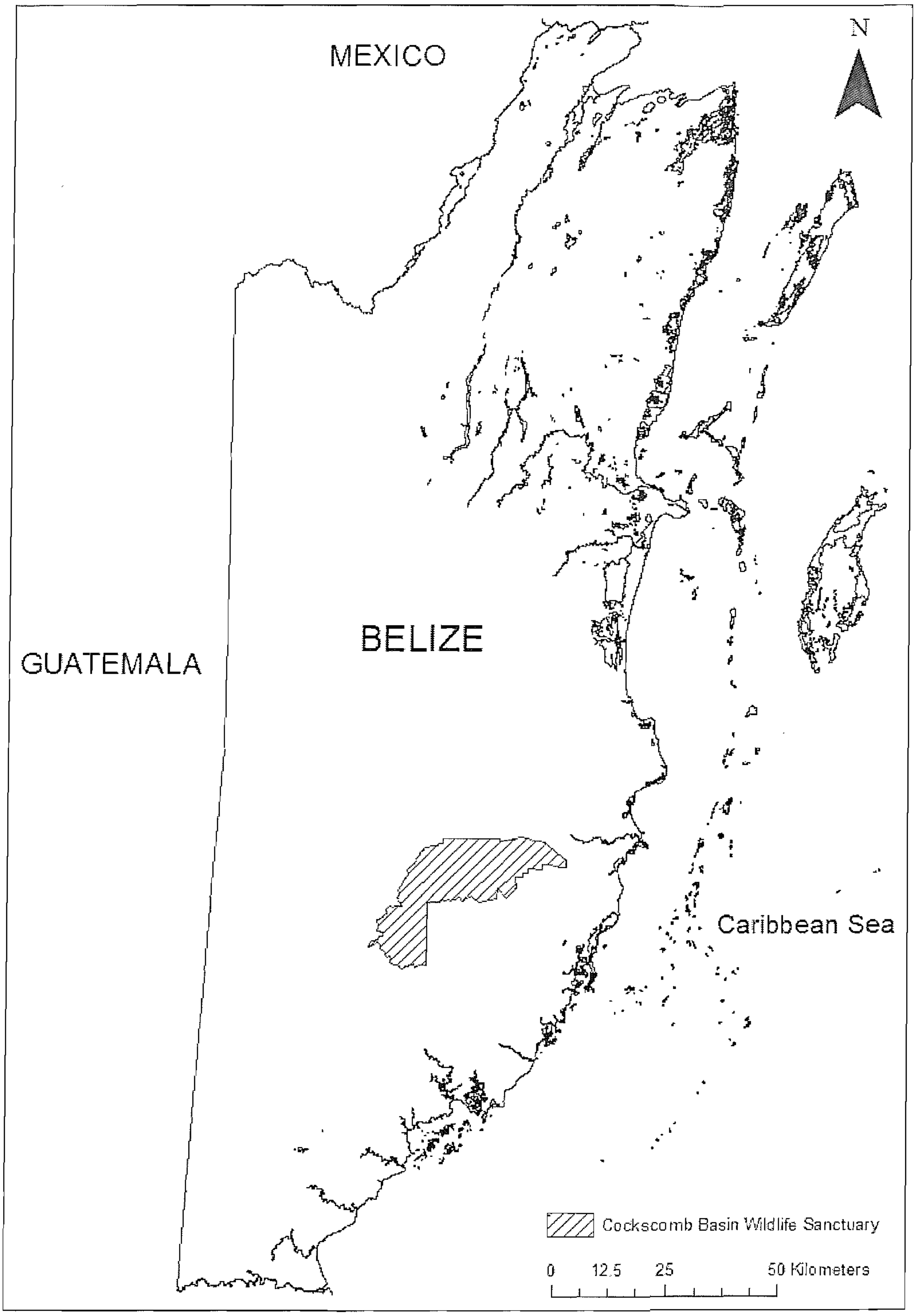


Figure 1.8 Map of Belize with the Cockscomb Basin Wildlife Sanctuary (CBWS).

# Chapter 2

# Methodology of camera trapping and mark-recapture analysis

# Introduction

Population management of any species requires accurate abundance estimates so that policy makers can determine sustainable levels of harvest or necessary levels of protection. Counting individuals in different areas reveals the distribution and abundance of a species across its range but simply knowing the population size is not enough to drive policy. Assessing whether a population is viable requires information on the potential long-term reproductive output; for cryptic species the easiest option is to monitor the population stability through time. This requires a method of estimating abundance that is both accurate (i.e. it reflects the true population size) and precise (i.e. the confidence intervals are small enough that change can be detected, Krebs 1994). This chapter discusses practical issues of setting up a camera trap study with special reference to abundance estimates using mark-recapture analysis. Camera trapping as a methodology was used throughout this study while mark-recapture analysis for abundance estimates was used in Chapters 3 and 4.

## *Methods of estimating abundance of large cryptic mammals*

Methods of estimating the abundance of large cryptic mammals must be both accurate and precise. They must be relatively quick and easy to use because prioritizing conservation areas cannot wait for several decades of research; finally the reality of conservation research is often one of limited funding, especially for species in developing countries, therefore the method must be cost effective. There are many methods to estimate large mammal abundance but few are appropriate for cryptic species such as jaguars.

### Invasive methods

Abundance of small mammals is frequently estimated directly from live-trap capture records. This method is not appropriate for large cryptic species such as jaguars. Cats in particular are wary of live traps and if caught once may become trap shy; as such sample sizes are too low to generate sensible estimates (see section mark-recapture). Also, small mammals have small home ranges therefore it is feasible to saturate a study area with live traps, the area and number of traps required to replicate such a study of big cats would be impractical.

Live capture, collaring and tracking using telemetry has been frequently used to study large elusive mammals. The home ranges and level of range of overlap of collared individuals are calculated from the telemetry data and used to estimate abundance and density in the study area. The method has been used widely for many different species and has been the main method of studying jaguars to date; although it is reliable and precise it is neither cost-effective nor efficient (see Chapter 1). Capturing a jaguar is labour intensive and expensive. All the published studies (see Chapter 1) have low sample sizes of ~5 animals; they are often conducted over a period of 2 years and require a lot of man power (dogs with hunters to tree the jaguar and/or staff to check and maintain live traps; veterinarians to anesthetise the jaguar, staff to track collared individuals) and expensive equipment (traps, drugs, collars and often light aircraft to search for collared individuals).

### Non-invasive methods

In contrast to invasive methods of estimating abundance, non-invasive methods are not reliable and precise enough to be used for absolute abundance estimates but they are quick, easy and cheap. Non-invasive methods utilise live sightings or signs of the target species (dens, footprints, markings or faecal material), for example distance sampling from line transects (Buckland 2001). Abundance estimates based on sightings are not appropriate for cryptic species such as jaguars since they are sighted rarely in the wild.

Jaguar footprints and scats can be found in the field and can be used for relative abundance estimates, for example to compare abundance between two areas. Sign survey data cannot be used for absolute abundance estimates. This requires knowledge of the relationship between sign frequency and known population size and such data are not available for jaguars. Even if the relationship were known it may be site specific due to the demography and social organisation of the particular population which may vary between locations (see Chapter 1).

## *Camera trapping as a method to estimate abundance of large cryptic mammals*

Neither live-trapping nor sign surveys are satisfactory for studying jaguars. Camera trapping combines the positive aspects of both the invasive and non-invasive methods. Remotely triggered cameras photograph the target species. If individual recognition is possible, and capture rate high enough, then mark-recapture analysis can be used to estimate abundance as in live-trap studies.

The use of camera traps in the life sciences is not new. In the early 20th century thin trip wires were used to mechanically trigger unmanned cameras in the field to photograph elusive animals. Tigers were photographed in this manner as early as 1927 (Champion 1927 in Karanth 1995). Griffiths & van Schaik (1993) were the first to recognise the potential of camera trap technology for the use of estimating abundance and replaced wires with pressure plates to electronically trigger cameras. More recently pressure plates have been replaced with heat and motion sensors.

Camera traps are well suited for presence/absence data and many rapid surveys are done throughout the world using camera traps for this purpose. The first study to use camera traps to estimate absolute abundance was conducted on tigers in Nagarahole, India (Karanth 1995). Tigers are individually recognisable from their stripe pattern. Karanth (1995) used mark-recapture analysis on the photographic capture data to estimate abundance, using the program CAPTURE (White et al. 1982; updated by Rexstad & Burnham 1991). CAPTURE was written for live-trap capture data but photographic captures can be used as long as the same assumptions hold (see later sections). Specific issues concerning the accuracy and precision of mark-recapture analysis of camera trap data are discussed in Chapters 3 and 4.

Camera trapping is becoming a major research tool for estimating abundance of large individually recognisable mammals that are otherwise difficult to study (Karanth & Nichols 1998, O'Brien et al. 2003, Kawanishi & Sunquist 2004, Maffei et al. 2004, Silver et al. 2004, Maffei et al. 2005, Miller & Miller 2005, Miller 2005). No data are presented in this chapter. The aim of this chapter is to outline the methodology of camera trapping as a reference for subsequent chapters.

# Methodology of camera trapping

Camera traps are either active or passive. Active camera traps are triggered when an animal actively breaks an infrared beam as it passes between two sensors on opposites sides of a trail. The system involves at least four separate components: two sensors, trigger box and the camera (e.g. Trail Master, Goodson Associates, Lenexa KS 66215, USA). Passive camera traps are triggered by heat-motion sensors. The motion-heat sensor consists of a row of plates that registers the ambient temperature. As a warm-blooded animal moves in front of the sensor the heat gradient alters and the camera is triggered. Passive cameras are sold commercially as a single unit containing the camera with a sensor below (e.g. Cam Trak Inc. 1050 Industrial Drive Watkinsville, Georgia 30677 US). The advantages and disadvantages of passive and active camera traps are compared in Table 2.1

Table 2.1 Comparison of active and passive camera traps.

| | **Active** | **Passive** |
|---|---|---|
| **Cost** | Expensive | Cheap |
| **Ease of assembly** | Difficult:Several components with wires between sensors | Easy: single unit |
| **Ease of operation** | Difficult for uneducated staff to operate | Easy for uneducated staff to operate |
| **Ratio target : non target photos** | Low: active sensor maybe triggered by falling vegetation or heavy rain | High |
| **Sensitivity to climate** | Only rain and wind not temperature changes | Not for rain and wind but heat blind if ambient temperature is high or target animal wet |

Both types of traps use 35mm film. Digital camera traps are becoming commercially available but the delay between the sensor triggering the camera and the camera focussing on the subject is too long to reliably photograph an animal before it passes the camera. Digital cameras use more energy than ordinary 35mm film cameras and this lowers the amount of time a camera can be left in the field even though digital cameras have a higher photo capacity.

Passive camera traps were chosen for this study (Cam Trak Inc.). Several models were used throughout the study period, January 2003 until June 2005, but the basic unit was the same: a weather proof box containing a commercial 35mm camera with automatic flash and a date and time stamp. The sensor was powered by 4 C-cell 1.5V batteries and the camera was either powered by these 4 C-cells or an independent camera battery (3V CR123). The batteries lasted 6 weeks for units with independent camera batteries and 3 weeks for the units with only C-cells. 35 mm 400ISO film was used in the cameras. Either 36 or 24 exposure film was used depending on the camera location and weather conditions: 36exp film was used in areas with high animal traffic to prevent film running out before it could be changed; however 36 exp film is wound more tightly than 24 exp film and tends to get stuck under very humid conditions so 24 exp film was preferentially used during the wet season.

## Camera placement

After identifying a suitable survey area from a map, camera locations were chosen in the field. The camera location must function as a funnel such that if the target species is nearby it will naturally choose to walk past the camera as there are no alternative routes in the immediate area. Trails were the most obvious funnel but in remote areas lacking trails, stream beds or game trails were used. In order to ensure that the camera trap "funnel" was the path of least resistance alternative routes were blocked with branches or loose vegetation.

Camera traps were preferentially placed near locations where signs of the target species had been found. For some surveys, maximisation of variation in microhabitat in the area was the objective. Signs were found infrequently off trail. If no signs of the target species were found then signs of prey species were used to select camera location. Areas at risk of flood were avoided, especially during the wet season when water levels can fluctuate dramatically. Despite this precaution camera traps did get flooded on a few occasions.

Once a camera location was chosen the trap was tied to a tree with wire. A post was cut and placed in the ground if there were no suitable trees. The trap was positioned so that the sensor was aimed across the trail. The height of the camera above the ground was chosen so that the sensor would be level with the chest of the target species, maximizing the surface area radiating body heat, increasing the chance of detection. The angle and height of the sensor was checked by crawling past the trap at the height of the target species (chest height of a jaguar is ~50 cm).

Depending on the survey either two cameras were placed opposite each other (double station) or just as a single unit (single station). Double stations were slightly staggered so that the flash of either camera would not interfere with the photo taken by the opposite camera; but close enough so that the animal would trigger both cameras within a few seconds of each other. This allowed the identification of both flanks, left and right, of the same individual by matching photographs taken at the same date and time. Double stations were also more robust against camera failure than single stations.

Single stations were only used during surveys that needed to maximise the number of trap locations. This was only done in areas which had been previously surveyed with some double stations so that there was already a double-side record of most of the individuals in the area.

### Checking cameras

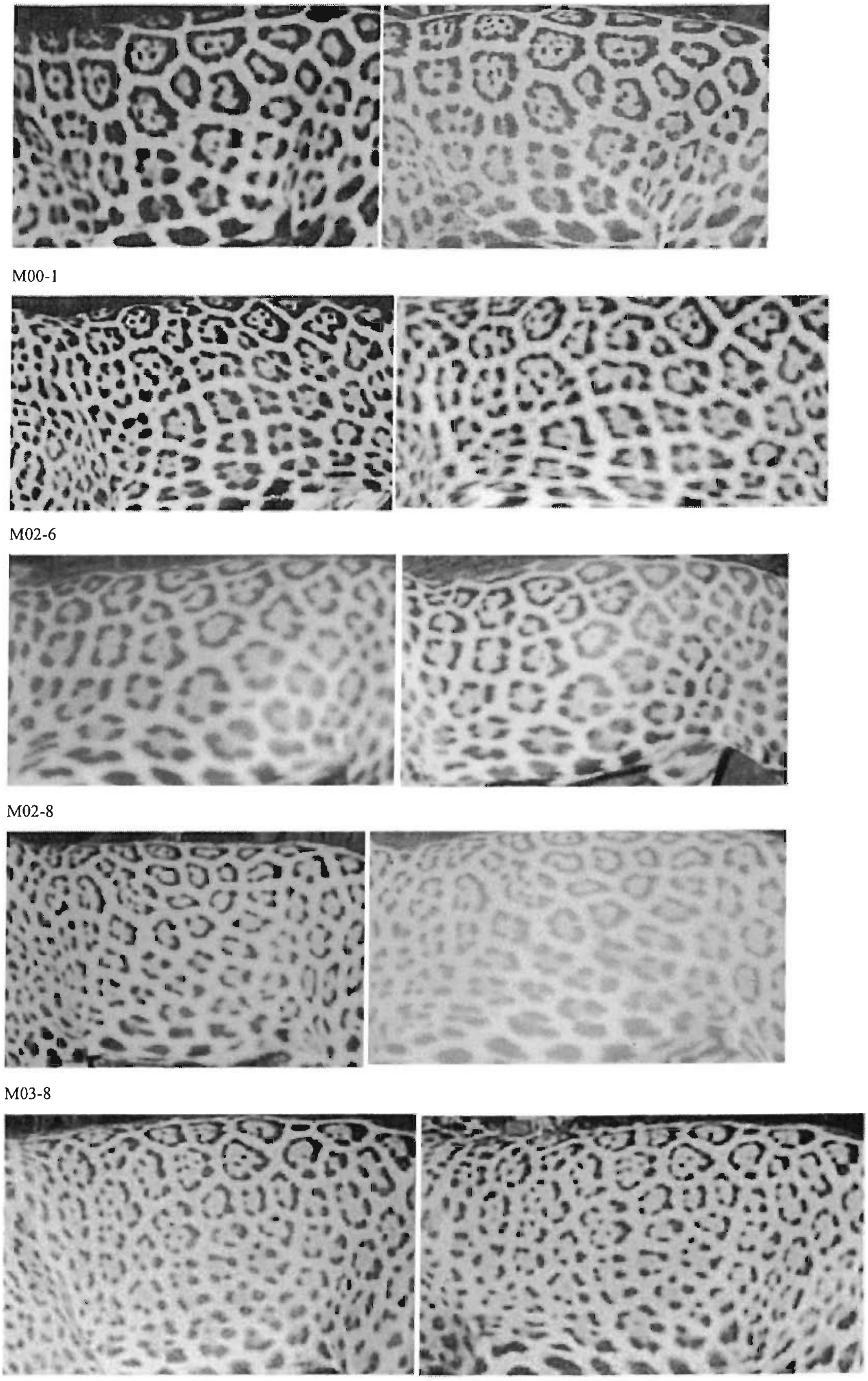
Camera traps were checked regularly to ensure that the cameras ran continuously throughout a survey. Batteries and film were replaced before they ran out. Cameras were checked at least every 2 weeks in remote sites with no human traffic and more frequently if many humans (tourists) were in the area. If camera traps malfunctioned they were replaced as quickly as possible. Film was marked with a unique identifier code for the location and start date before it was put into the camera. Films were developed in country throughout the duration of the study.

## *Individual recognition of jaguars*

The rosette and spot patterns of jaguar coats are unique to individuals and easily distinguished by eye. Although the overall pattern is generally similar between the two flanks of the same individual it is not symmetrical, either flank is different. For this reason, pattern comparison is only done on a single flank, i.e. left flank photographs are compared with other left flank photographs (head facing to the left, tail to the right) and right flank photographs are compared with other right flank photographs (head facing to the right, tail to the left).

A right flank photograph can only be matched to a left flank photograph if the photographs are taken simultaneously at a double station. Figure 2.1 shows examples of coat patterns of five individual jaguars (Figure 2.1a matching left flanks and Figure 2.1b matching right flanks of the same individuals). The overall rosette patterns are similar between the left and right flanks but not enough for individual recognition. As can be seen in Figure 2.1, the position of limbs and angles of photographs can distort the pattern slightly; and the appearance of rosettes can vary with the sharpness of the photograph.

At the end of a survey photographs of each flank were compared with each other and grouped by matching unique patterns (different individuals). After this process, the left and the right flanks were matched according to trap location, date and time. Once a match was made between a left flank and a right flank then all subsequent photographs of either flank could be matched to the individual. For survey purposes the only problem that can arise is if single right and left flank photographs are unmatched by date and time (for example due to failure of a camera at a double station). In this situation one cannot be certain if these individual left and right flank photographs are from one or two individuals. This situation never occurred in the present surveys. The dates and times when individual jaguars were photographed were now used as an input for mark-recapture analysis.



M00-1

M02-6

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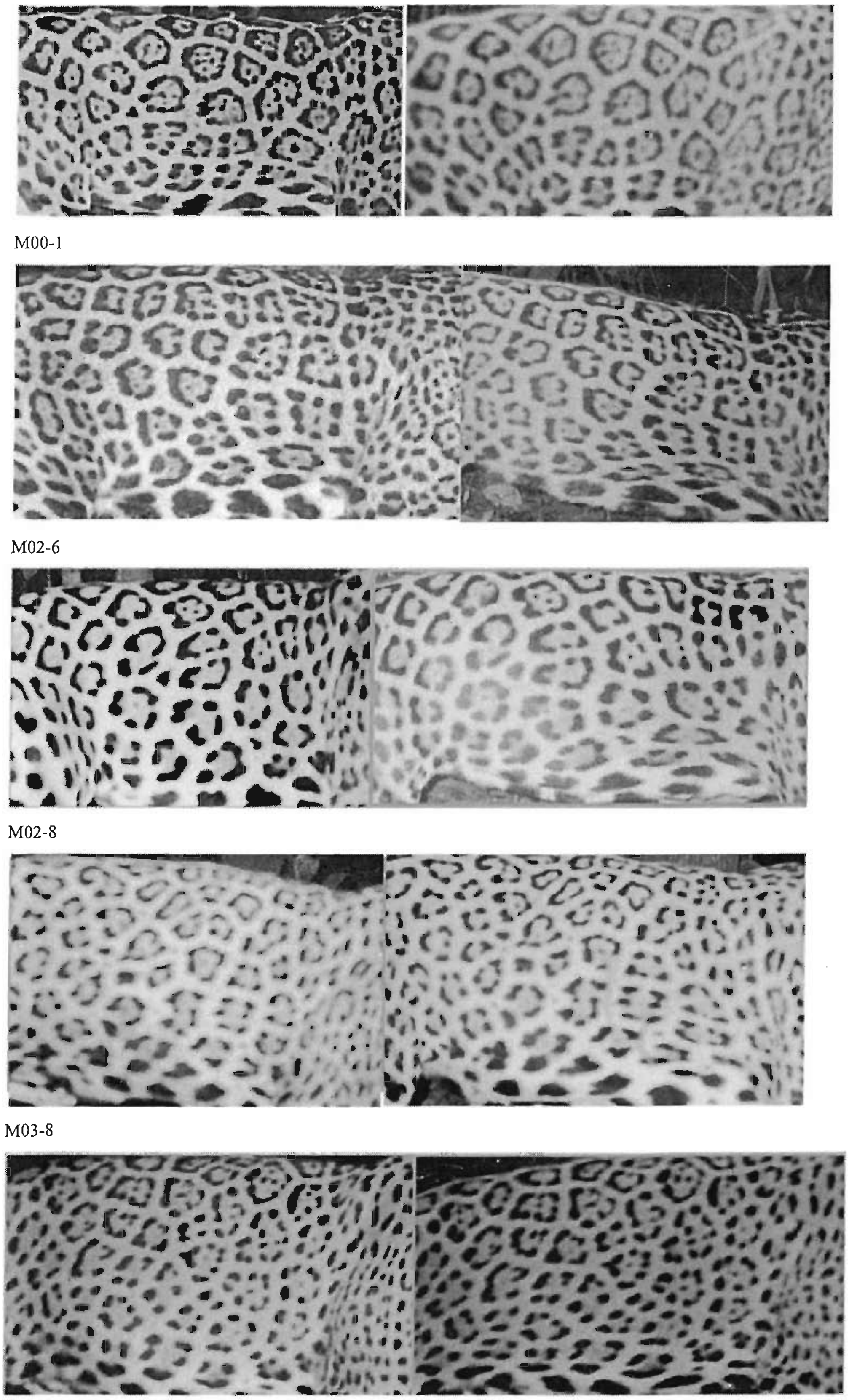
M03-8

M02-5

Figure 2.1a Examples of two matching left flanks for five individual jaguars The codes underneath the picture are the jaguar IDs.



M00-1

M02-6

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M03-8

M02-5

Figure 2.1b Examples of two matching right flanks for five individual jaguars (same individuals as for Figure 2.1a). The codes underneath the picture are the jaguar IDs.

## *Individual recognition of pumas*

The puma lives sympatrically with jaguar throughout most of its range (see Chapter 1). They are of similar size and height as the jaguar and have similar ecological requirements (see Chapter1). Camera traps positioned to photograph jaguars are suitable for pumas in terms of location and height of camera.

Unlike the jaguar, the puma is uniformly brown and lacks obvious uniquely distinguishable features. Attempts were made to recognise individual pumas. It is easier to see wounds and scars on pumas than it is on jaguars. Wounds and scars are a temporary but they may be used during a single survey as a method of individual identification (Figure 2.2a). Pumas are regularly observed infested with botfly larva (*Dermatobia hominis*). Large lumps, approximately 25 mm diameter, are visible on the body for > 2weeks providing a temporary and uniquely identifiable pattern (Figure 2.2b).

Although not as distinct as the jaguar rosettes, pumas have dark shading under their fore and hind legs that could be distinctive. Additional features were used to try and identify individual pumas, such as kinks in tails (Figure 2.2c), black markings on the tail and residual juvenile markings (Figure 2.2d). In addition, overall body shape and size were used as additional identifiers (although not as the only method of identification).

Individual recognition of pumas was not possible for entire surveys during this study. Pumas could be identified in certain areas for limited periods if the sufficient identifiers were present. Photographs of individuals lacking distinguishing features were too frequent to allow individual recognition for a complete survey. Frequency data of puma photographs and limited individual recognition data was used in Chapter 6 and Chapter 9.

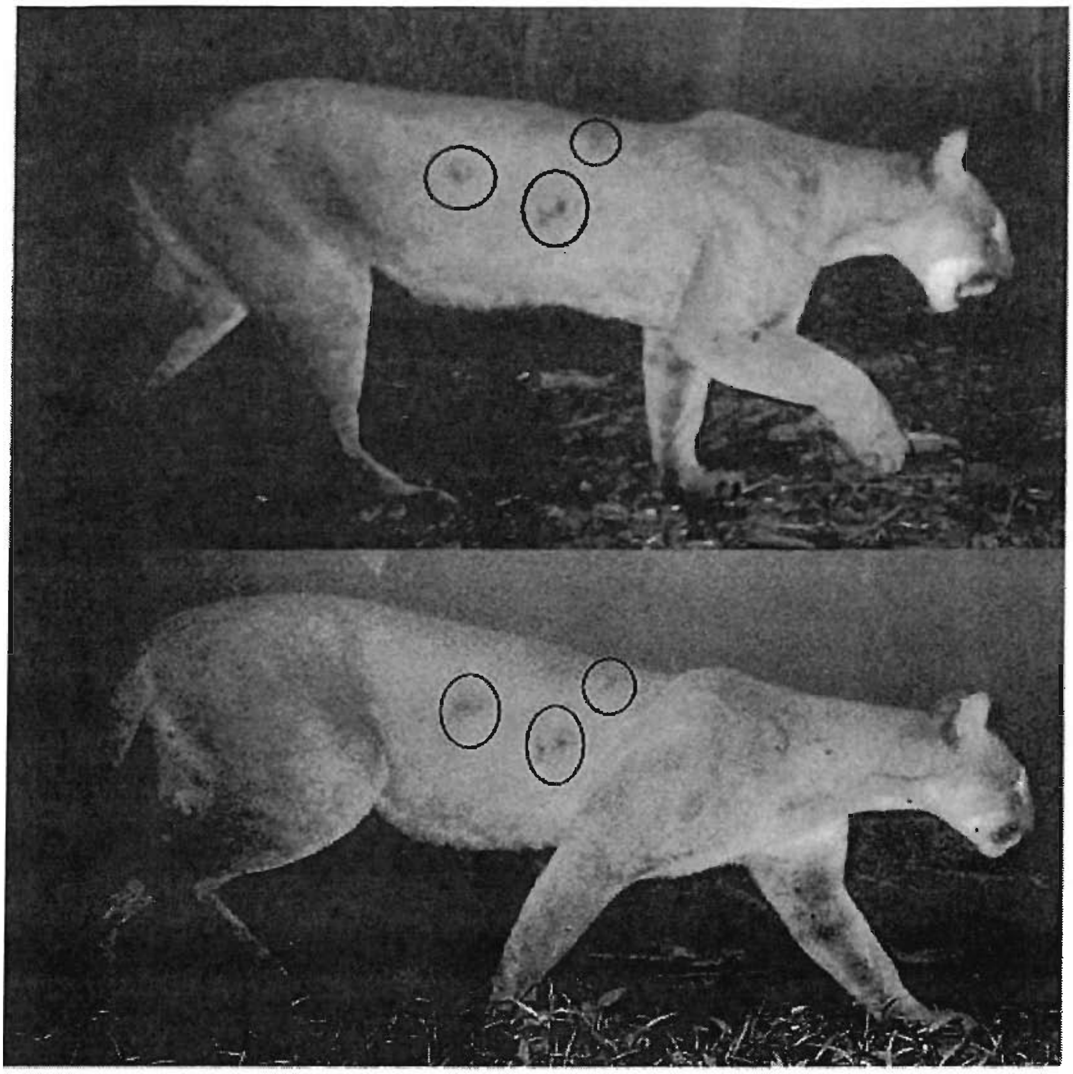

Figure 2.2a Example of a puma identified as the same individual through the scar pattern on its flank (time interval between photos is 18 days).

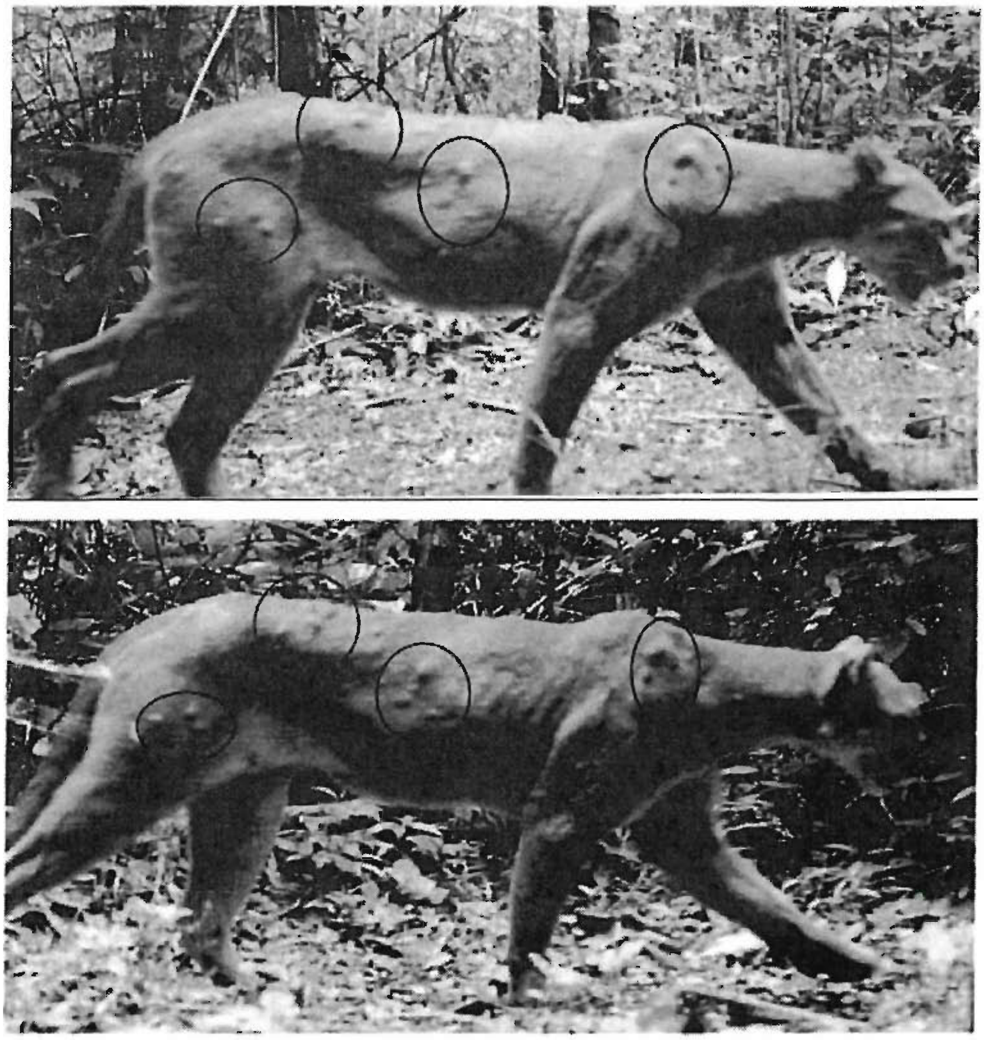

Figure 2.2b Example of a puma identified as the same individual through the botfly larva pattern on its flank (time interval between photos is 11 days).

Figure 2.2c Example of a puma with a broken tail. The high number of spots on the side of this puma are botfly larva.

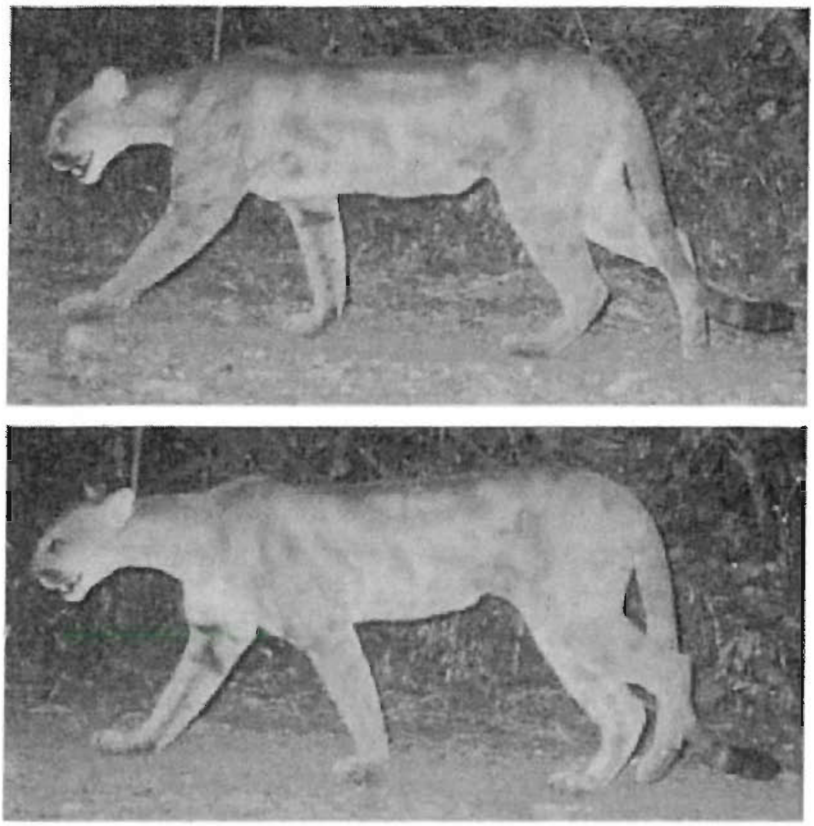

Figure 2.2d A rare example of a puma with markings. Adolescent pumas tend to have vague spot markings which fade as with age (puma cubs have spots). The markings have not faded on this individual who has been captured over a period of 3 years.

## *Estimating abundance from camera trap data*

Mark-recapture analysis, using closed or open population models, is used to estimate abundance from capture records. Closed population models allow accurate estimation of population size with confidence intervals. The confidence intervals are relatively small and the sampling periods are relatively short (Krebs 1994).

Open population models are more complicated, but became more workable with the advent of computers. In addition to estimating population size, open population models can be used to calculate recruitment and survival rates. They require several sampling periods over a longer time period than do closed population models. They are more suited for long term studies since the sampling periods have to make biological sense in terms of lifespan of the animal (Krebs 1994). For jaguars this means that the sampling periods have to be at least a year apart to estimate reliable survival and recruitment rates. For these reasons, closed population models are preferable. The use of closed population models for the estimation of jaguar abundance is discussed here. Open population models are discussed in Chapter 5.

## Assumptions and limitations of closed population models

The computer program CAPTURE uses closed population models that are variants of the "ball & urn" model in which the number of balls in an urn is estimated by drawing a sample of balls, marking and returning them to the urn, then withdrawing a second sample and comparing the ratio of marked to unmarked balls. Certain assumptions about the study population must be met in order to use the "ball & urn" model to reliably estimate animal abundance (for reviews of mark-recapture literature see White et al. 1982, Pollock et al. 1990). First, the sampled population must be closed. No immigration, emigration, deaths or births can occur during the survey period (*no balls can be added or removed from the urn while sampling*). Second, all individuals should have equal trapability. This must be true for previously captured (marked) individuals and newly captured (unmarked) individuals (*all balls have an equal chance of being drawn, and once they are marked they should have the same chance of being taken on subsequent draws*). This requires that sampling is random (*the balls in the urn must be mixed thoroughly between draws*).

The two assumptions of the "ball & urn" model translate into five assumptions in the field for mark-recapture estimates using Petersen and Schnabel estimators of closed populations (Krebs 1994):

1) The population is closed so that $N$ (total population) is constant.
2) All animals have the same chance of capture in the first sample.
3) Marking individuals does not affect their catchability.
4) Animals do not lose marks between sampling sessions.
5) All marks are noted upon discovery in subsequent sampling occasions.

The final two assumptions are irrelevant for camera trap studies since the unique coat pattern rather than artificial marks are used to identify individuals. The first three assumptions require further attention.

1) Closed population

a) Demographic closure requires that no deaths or births occur during the survey period. The assumption can usually be satisfied if the sampling period is relatively short. In studies of long-lived species such as big cats a sampling period of 2 months is considered valid (e.g. Karanth 1995, Silver et al. 2004). The assumption can be relaxed if mortality rates do not differ between marked and unmarked animals (White et al. 1982).

b) Geographic closure requires that no individuals move into or out of the area during the sampling period. Again, a short sampling period will satisfy this assumption. Big cats have relatively fixed home ranges. It is unlikely that major social changes will take place within a short sample period (for example territory shifts or new animals moving into unoccupied areas due to mortality). This does not account for transient individuals passing through the area, but the model is relatively robust if only 1 or 2 individuals sampled are transient when the sample size of individuals is > 10 (pers. comm. J. D. Nichols, senior scientist, USGS Patuxent Wildlife Research Center).

The program CAPTURE tests for statistical closure (Z-test). This test cannot statistically distinguish time effects, for example, increased capture rate due to environmental conditions, or behavioural effects, for example, individuals becoming trap happy or trap shy, in the trapping records as distinct from a real violation of closure. The only way to ensure that the assumption of closure is satisfied is to keep the sampling period short, test for statistical closure and scrutinise the data for potential transient individuals to detect evidence for violation of closure.

2) Homogenous capture rates

In a real population there is almost always heterogeneity in capture rates between individuals, for example due to territoriality within the sampling area, social status etc and this phenomenon has been well documented in the literature (White et al. 1982). The JACKKNIFE model ($M^h$), available in the program CAPTURE, has been developed to estimate population sizes in closed populations with heterogeneous catchability. The derivations of the model are complicated and well beyond the scope of this chapter (for more detail Otis et al. 1978 in Pollock et al. 1990). Potentially the model can have as many parameters as number of individuals. Although the JACKKNIFE model allows relaxation of the assumption of equal catchability it does assume that each individual's catchability coefficient ($p^i$) remains stable throughout the survey period.

3) Catchability is not affected by marking

This assumption states that the catchability remains stable after the initial capture. Under the JACKNIFE model heterogeneity in capture rates is allowed but it must be stable throughout time. In reality capture rates may change through the survey period due to temporal extrinsic factors and behavioural factors:

Catchability may change throughout the sampling period due to external circumstances, for example changes in weather can alter food availability and therefore alter the attractiveness of bait in live traps. Similarly weather can affect the functioning of camera traps and so influence catchability. The program CAPTURE allows for time differences using a variant of the Schnabel multi-catch closed population model, the DARROCH model ($M^t$, for more detail see Otis et al. 1978 in Pollock et al. 1990). Each capture event can have its own catchability rate ($p^t$). This is constant per capture event for all individuals captured within that event, i.e. all individuals captured on a single day have the same catchability $p^t$. The DARROCH model does not allow heterogeneity in capture rate between individuals so a combination of time effects and heterogeneity cannot be combined in this model.

Trapping may alter an individual's behaviour and so influence their chance of subsequent trappings. It has been well documented in literature that animals can become "trap happy" or "trap shy" following capture (White et al. 1982). It is unlikely that individuals will become "trap happy" around camera traps since there are no food rewards as used in live-trapping. The cameras flash at night and this may frighten individuals, in effect making them "trap shy". The program CAPTURE can take into account such behavioural variations, such that catchability can increase or decrease following first capture, using the ZIPPEN model ($M^b$, for more detail Otis et al. 1978 in Pollock et al. 1990). In this model the catchability of individuals at first capture is constant for all individuals and subsequent capture rates are also constant depending on the number of previous captures of the particular individual.

The program CAPTURE allows a behavioural response in combination with a population of animals with heterogeneous catchability ($M^{bh}$) using the REMOVAL model (for more detail Otis et al. 1978 in Pollock et al. 1990). It is based on removal experiments in which populations are estimated by removing individuals from the population and studying changes in the catchability of remaining individuals. In this case the marked individuals are "removed" from the unmarked population. This model can be used for estimating abundance in a situation in which behavioural effects and heterogeneity in capture rates are likely since it only uses the first trapping occasion of each individual. Removal models assume constant capture rate over time and for this reason a full $M^{bht}$ model cannot use the removal method.

The program CAPTURE tests mark-recapture data for heterogeneity, time effects and behavioural effects. $\chi^2$ tests test the goodness of fit of the different models against each other. The most commonly used model in camera trap data, with the highest fit and making most biological sense, is the JACKKNIFE model allowing for heterogeneous catchability among individuals (Karanth & Nichols 1998, O'Brien et al. 2003, Kawanishi & Sunquist 2004, Maffei et al. 2004, Silver et al. 2004, Maffei et al. 2005, Miller & Miller 2005, Miller 2005). The JACKKNIFE model is also more robust against violations of the assumptions than are the other models. Heterogeneity of capture does not allow capture rates of many individuals to be extremely low ($p^i <$ 0.1). Simulation studies using CAPTURE showed that the population estimate tends to be unreliable when many individuals have extremely low capture rates (White et al. 1982). Every individual must have a catchability coefficient > 0. CAPTURE generates an estimate of the overall catchability $\hat{p}$ .

In conclusion the following assumptions must be satisfied in order to use CAPTURE mark-recapture models of camera trap data to estimate population abundance:

1) The population must be demographically and geographically closed although the models are robust against minor violations.

2) Every individual must have a catchability higher than zero and the total catchability rate should be higher than 0.1.

### Confidence intervals of abundance estimate

One of the advantages of using a program like CAPTURE to estimate abundance instead of using an abundance index is that it calculates confidence intervals of the estimate. This is important since abundance estimate will always have a level of error, which must be reported to understand the value of the data.

CAPTURE calculates the standard error (s.e.) of the estimate and the 95% confidence intervals (CI).

Estimates generated from capture records with low $\hat{p}$ values tend to have CI with the lower half below the number of recorded individuals if the CI are calculated as ± 1.96 × (s.e.). CAPTURE corrects for this by recalculating the CI in the following manner (Burnham 1992):

It is assumed that individuals in the population that are not captured $(N\text{-}M_{t+1})$ have a log-normal distribution. $N$ is the estimated population size and $M_{t+1}$, is the number of individuals captured. The confidence intervals are calculated as:

Lower: $M_{t+1} + \frac{N - M_{t+1}}{C}$ Upper: $M_{t+1} + (N - M_{t+1}) \times C$

$C$ is a constant that is calculated as:

$$C = e^{1.96\sqrt{\log\left[1 + \frac{VarN}{(N - M_{t+1})^2}\right]}}$$

These calculations can create skewed confidence intervals with the mean close to the lower half of the confidence interval since it is impossible for the lower bound to fall below the number of captured individuals.

### Conversion from camera trap data to capture matrix

Camera trap data are converted into a CAPTURE matrix: individuals in the rows and trapping occasions in the columns. Each row represents one individual and each column represents one trapping occasion (e.g. one 24-hr period). In Chapter 3 more attention is given to the choice of trapping occasion. Capture of an individual within a trapping occasion is signified with a "1", non-capture with a "0". Figure 2.3 shows the matrix for the 2002 large-scale survey. Eleven individual jaguars were captured (A to K) over 59 trap occasions (days). The record has a high number of non-captures. The abundance estimates have no spatial component. CAPTURE does not distinguish between captures at the same or different locations.

| | |
|---|---|
| A | 00010000000000000000000000000000000000000000000000000000000 |
| B | 00001100000000000010110000000000011000000000100001001100100 |
| C | 00001000010000010010000110000000000000100000000000000000000 |
| D | 00000000000000000010000000000000001000000000000000000000000 |
| E | 00000000000000000001000000000000000000000000000010010000000 |
| F | 00000000000000000001000000000000000000000000000000000000000 |
| G | 00000000000000000000001000010000000000000100000000001000000 |
| H | 00000000000000000000000000000001000000000100000000000000000 |
| I | 00000000000000000000000000000000000000000010000000000000000 |
| J | 00000000000000000000000000000000000000000000000000001000000 |
| K | 00000000000000000000000000000000000000000000000000000000001 |

Figure 2.3 CAPTURE matrix for 2002 large-scale survey. Each column represents a day (59 days in total) and each row represents an individual jaguar (11 individual jaguars, A to K). Rows are ordered by date of first capture.

## *Estimating density*

Abundance estimates can be standardised to compare between areas by calculating density (number of individuals per km$^2$) If the survey area cannot be calculated then the abundance estimate can only be compared with other estimates from the same area through time. The simplest area measures are calculated for geographically closed populations: fish in a pond, animals on a small island etc. If the entire closed area is sampled then density ($D$) is calculated as the estimated population ($N$) divided by the closed area ($A$): $D = N/A$.

For many species of large mammal this is not possible. It would be logistically impossible to sample the entire area utilised by a single jaguar population. For this reason small areas are sampled within the population. Without the use of radio-telemetry or very extensive camera trapping there is no way of knowing how far home ranges of individual jaguars extend beyond the study area demarcated by the outer camera traps. The problem of individuals only partially living within the sampled area is different from immigration and emigration. Such individuals do have capture probability > 0 for all trapping occasions; although it is lower than that of an individual whose home range is entirely encompassed by the study area. For this reason the JACKKNIFE model is the most appropriate model for abundance estimates of mammal populations containing individuals with home ranges that likely extend beyond the study area.

The problem of home ranges extending outside of the study area is well documented (White et al. 1982). The effective sampling area is the area utilised by the individuals that are sampled, the total study area is the area surrounding the outermost traps. If the ratio of study area to average individual home range is large then the density can be calculated by the area bounded by a polygon drawn around the outer most traps (total study area). In this case the size of the effective sampling area (area utilised by the individuals that are sampled) is negligibly larger than the total study area (Figure 2.4 left). The lower the ratio of study area to home range size, the higher the difference between effective sampling area and study area. Figure 2.4 gives three examples of study areas (large squares) and home ranges of animals in the area (ellipse shapes). Figure 2.4, left shows a non biased site: small home ranges in a large study site, Figure 2.4, middle shows a study site with medium bias: larger home ranges in a smaller study site and Figure 2.4, right shows a study site in which the home ranges are large compared to the study site. Here the effective sampling area is much larger than the study site. The case for jaguars and tigers is probably best represented by Figure 2.4, right, meaning that there is substantial difference in trapping area and the effective area sampled. Using the study area for density calculation would greatly overestimate the density in this case.

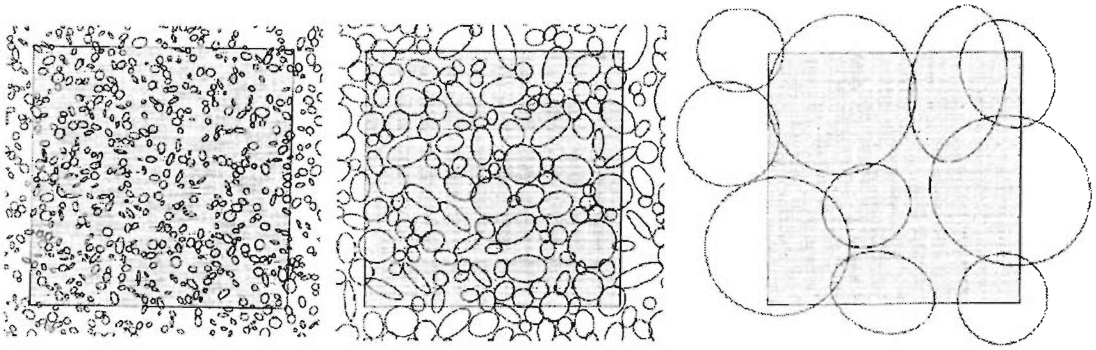

Figure 2.4 examples of a study areas (large squares) supporting home ranges (ellipse shapes) of different sizes. Ratio of home range : study area increases from left to right (Source White et al. 1982).

The effective area covered by a survey can be calculated from the mean maximum travel distance of the sampled individuals (MMDM, mean maximum distance moved). The MMDM gives an estimate of how far on average individuals roam from any camera location. The effective area can be calculated by adding a buffer strip to the study area. The buffer is a circle around the outermost cameras of the study area with a radius that is half the MMDM. Telemetry data would be the most reliable method to estimate the MMDM but camera trapping is generally utilised in order to avoid the need for telemetry. Wilson & Anderson (1985) used an ad hoc approach to calculate the MMDM that performed well in simulation studies. It is based on the MMDM of all the animals that are trapped twice or more. The maximum distance between capture locations is calculated for each individual. The mean of the maximum distances for all the individuals is then calculated. This method was used by Karanth & Nichols (1998) for the calculation of effective area of tigers and subsequently followed by many other researchers.

$$d = \sum_{i=1}^{m} \frac{d_i}{m}$$

*d* is the mean maximum distance moved, $d_i$ is the maximum distance moved for individual i and m is the number of individuals with more than two capture records.

The variance of *d* is:

$$Var(d) = \frac{\sum_{i=1}^{m} \left( d_i - d \right)}{m(m-1)}$$

Buffer strip (*W*) is calculated as half the mean maximum distance moved: $W = d/2$. The variance of *W* is $var(W) = 0.25 \times var(d)$.

The buffer strip is added to the sample area based on the outer points of the camera grid giving an estimate of the effective sample area *(A(W))*. In the case of camera traps this is done by adding a circle of radius *W* around each camera trap. The total area *A(W)* is the total area covered by the circles in the study area. In this study the *A(W)* was calculated using the program Arcview 3.2.

Density is calculated as: $D = N/(A(W))$.

The variance of the density is calculated as:

$$Var\ D = D^2 \left[ \frac{\mathrm{var}(A(W))}{(A(W))^2} + \frac{\mathrm{var}(N)}{N^2} \right]$$

All these variables can be calculated from the camera trap data. The program CAPTURE provides $N$ and its variance. Only the variance $(A(W))$ needs to be calculated separately. Karanth & Nichols (1998) recommend that the study area be approximated by a circle with a radius $c+W$, where c is a constant. $A(W)$ is then approximated in the following way:

$$A(W) = \pi(c + W)^2$$

With this approximation, a delta method is used to approximate $var\,A(W)$ (Karanth & Nichols 1998):

$$var\,A(W) = 4\pi^2(c + W)^2\,var\,(W)$$

There are still problems with the method since it requires the study area to be large enough to adequately sample the maximum distance moved. Estimation of the MDMM is limited by distance of the largest distance between the furthest cameras. This is not dealt with in this study since estimating the minimum study area requires extensive study areas and resources. It is reasonable to assume that MMDM is relatively stable for areas of similar prey distribution and topography. In this study the mean of the MMDM (calculated each year over 4 years) is used as to calculate $W$ as one fixed value. This value is used throughout the study. In Chapter 3 density estimates based on the MMDM for each survey separately are compared with those based on the mean MMDM over the 4 years combined.

## *Camera trap survey design*

Two types of camera trap surveys were conducted during the study period: large-scale surveys to estimate abundance and short-term concentrated surveys to study the effects of trapping effort. This section describes the design of the large-scale surveys; the results of these surveys are presented in Chapter 3. The short term surveys are discussed in Chapter 4.

## Duration of the study to satisfy the closure assumption

To satisfy the closure assumption the period of study has to be relatively short, however it should not be too short because trapping success of jaguars is relatively low due to the low density at which they live. For tigers and jaguars 2 months is the standard trapping period (maximum 3months, Karanth & Nichols 1998, Maffei et al. 2004, Silver et al. 2004, Miller & Miller 2005, Miller 2005). To date, four large-scale surveys were carried out in the CBWS. Table 2.2 gives the logistic data for each four surveys. Originally the start date was to be fixed at the start of February but due to logistical problems (camera failure or volunteer projects in the CBWS) the surveys were often delayed; even so all the surveys fell within the dry season.

Table 2.2 Timing and duration of four large-scale jaguar surveys in the CBWS.

| Survey year : | 2002 | 2003 | 2004 | 2005 |
|---|---|---|---|---|
| **Start date** | 1-Feb | 5-Feb | 29-Feb | 22-Mar |
| **Number of days** | 59 | 65 | 72 | 77 |

## Distance between camera traps

The assumption that every individual has a catchability > 0 can be satisfied by ensuring that the distance between camera trap locations is small enough such that the home range of a single individual cannot exist in between neighbouring camera locations. In other words, every individual within the study area should have at least one camera trap within its home range. The smallest known home range of jaguars in this area is 10 $km^2$ (Rabinowitz & Nottingham 1986). To estimate the minimum distance required between camera traps, a circle of 10 $km^2$ was drawn around each camera location. Circles of neighbouring cameras had to touch and preferably overlap. If there are gaps between camera circles then, in theory, an individual with a home range of 10 $km^2$ could live between the camera locations and have a zero chance of capture. Figure 2.5 shows the survey with 10 $km^2$ circles drawn around each camera trap location.

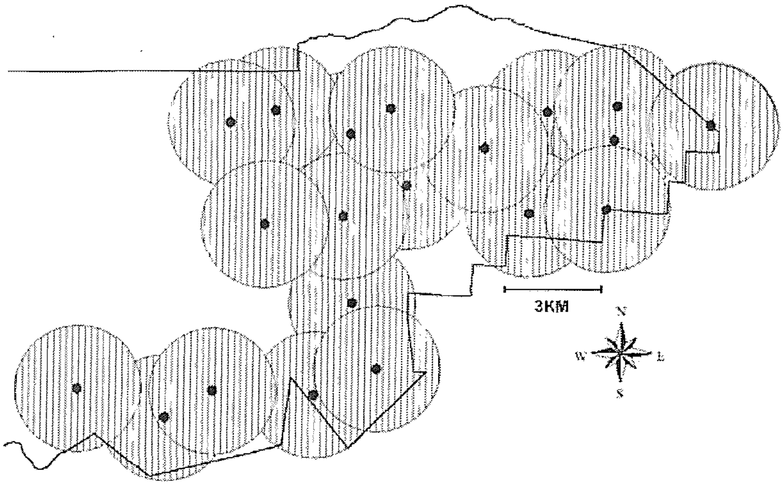

Figure 2.5. Boundary of the CBWS (black outline) with the camera locations (dots) of the large-scale survey each with 10 km$^2$ circles around it (shaded area).

The design shown in Figure 2.5 above is based on the maximum spread of cameras to cover the largest area possible with the available resources. Smaller distances between cameras would be preferable since this would lower the chance of breaking the assumption of zero catchability. In Chapter 4 smaller, higher trap density survey designs are used and the effect of smaller distances between cameras is discussed.

## Size and shape of the survey area

The size of a study area is mainly dictated by logistics and less by scientific inference. For an species such as a jaguar a study area that encompasses the home range of a large number of individuals (~ 50) would be ideal but is simply impossible in a dense jungle environment. Cameras, batteries and film all have to be carried by foot. As such the study area is dictated by the available man-power and how many cameras can be visited within the required checking interval. The effective sample area in this study was between 160-230 km$^2$. The size of the area is larger or similar to study areas used for other jaguar and tiger camera trap studies (e.g. Silver et al. 2004, Karanth & Nichols 1998).

The shape of the camera grid is an important consideration. In many small mammal studies the trapping grids are square or rectangular. The aim is to minimize the ratio of the boundary to area of the chosen study area. The smaller the ratio of boundary to area of the grid, the smaller the difference will be between effective area sampled (with added boundary strip) and study area grid. For this study the choice of shape of study area was poor (see Figure 2.5) with an extremely large boundary to area ratio. For the survey 40 camera traps were available for 20 double stations, in subsequent years only 38, one station was removed because of frequent flooding. The present design for the 2003, 2004 and 2005 surveys was chosen so as to replicate the first survey in 2002 (Silver et al. 2004). The 2002 survey design was based on logistic considerations. A grid survey was envisioned but had to be modified due to heavy poacher traffic in certain areas which put camera at risk of theft and vandalism. Only two main trails lead into the forest (old logging roads). Creating additional trails could facilitate poaching. Established trails often have high trap success of jaguars compared to cameras placed in the middle of a jungle matrix away from main trails (see Chapter 4). As such the main core of the survey was designed around two large established forest trails. These two trails were connected by trails cut especially for the study that had no direct connection to existing trails outside the CBWS boundary.

### Changes in camera locations between large-scale surveys

Several camera locations were altered between the large-scale surveys. Throughout the years, five of the twenty stations changed location, sometimes with dramatic effect on trap success (stations 5, 10, 13, 17 and 20 in Figure 2.6). They were only moved ~100 m from their original locations and so the overall survey area was not affected.

Four positions were altered after the 2002 survey and remained constant for the subsequent surveys (stations 5, 10, 13 and 17 in Figure 2.6). These four positions had no jaguar activity in 2002 but had high to fair trap success following the change. They all entailed moving cameras from narrow freshly cut trails to established trails.

The fifth location was moved in 2004 (station 20). Originally this was at the edge of the study area on a narrow trail leading to a stream, near the main access road into the CBWS (unpaved dirt road used by wardens and tourists to drive in). This road frequently has jaguar sightings and the camera on the small trail captured just 1 jaguar in 2002 and no jaguars in 2003. The camera was put here rather than on the access road to avoid it rapidly running out of film as vehicles passed. In 2004 it was moved to the road and set to operate only at night when the vehicle traffic is low. Although the rare daytime appearance of a jaguar on the road may have been missed this was offset by high night-time capture rates here compared with the original location. This camera location, monitoring the access road, was used in the 2004 and 2005 surveys.

Station 14 was removed from the study after 2002. The camera was originally put on a side stream near one of the main rivers of the CBWS. The cameras were flooded, even during the dry season, since the whole area is a flood plain, and the camera location was removed from the survey.

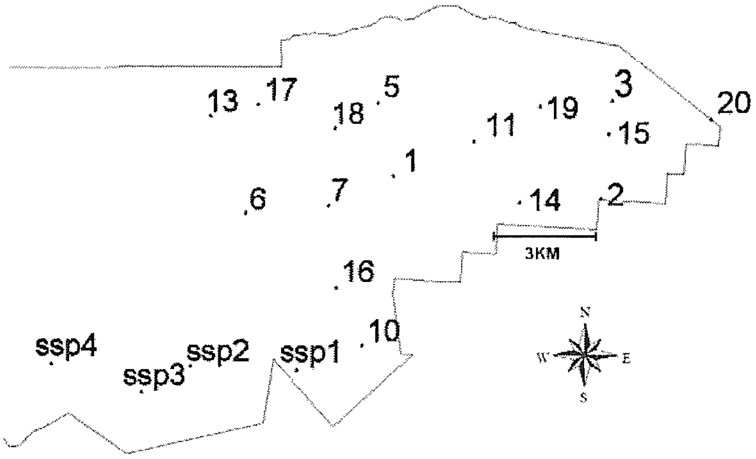

Figure 2.6 Boundary of the CBWS (black outline) with the locations (dots) and ID of the cameras of the large-scale survey (similar as in Figure 2.5).

## Habitat information of the survey area

The relation between camera trap success and several habitat variables are explored in Chapter 4. Figure 2.7 shows a satellite image of the CBWS giving information on vegetation, elevation, water ways, roads and main forest trails. The 20 large-scale survey camera locations are shown for reference. The names of five areas within the study area are included on the map, these areas are frequently referred to in subsequent chapters. Juan Branch is the only area that falls partially outside of the CBWS boundary.

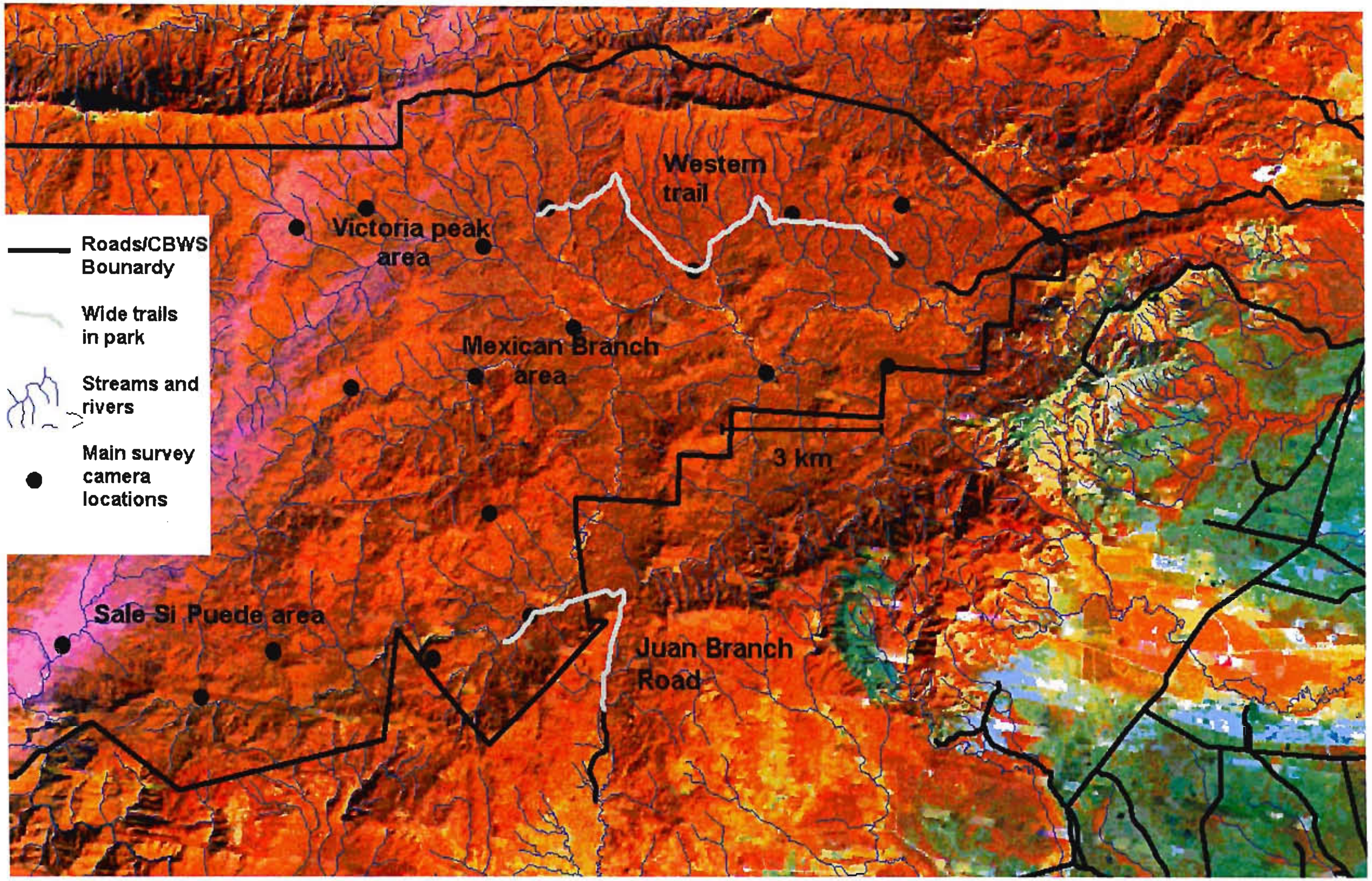

Figure 2.7 Satillite photo of CBWS area (Meerman 2003). The dark brown area is thick jungle vegetation, lighter brown area is very low canopy secondary jungle or citrus plantation and light green is savannah area. The shadow cast by mountains give an idea of elevation and slope within the area

# Chapter 3

# Influence of catchability on abundance estimates of jaguars

## Abstract

The widespread and increasing use of abundance estimates generated from mark-recapture analysis of camera trap data requires assessment of reliability. This is the first study to test the reliability of mark-recapture analyses, revealing potential biases in most published studies. Simulation models indicated a threshold of capture rate and heterogeneity of capture rate below which studies generated unreliable estimates. Most published studies fell below this threshold. Here we report the first long term camera trap study with repeated surveys. Re-sampling of these data indicated that abundance estimates could be biased by variation in survey length and minor changes in camera locations. The study introduces new guidelines for future research to ensure reliability.

## Introduction

A fundamental prerequisite of conservation management is to have knowledge of the abundance of the target species within an area. Estimation of population size for rare species requires robust and efficient methodology that, when applied correctly, provides reliable estimates of abundance for target populations. Chapter 2 introduced the method of camera trapping, with the mark-recapture analysis. Camera trapping is currently the main method used to study elusive medium to large sized mammals living at low density. The aims of the present study are to assess the limits of usability of mark-recapture studies for low density populations in terms of catchability, and to present recommendations for future studies to avoid pitfalls arising from inappropriate choice of survey length and trap locations.

Many studies have used camera trapping and mark-recapture as if it were a fully validated tool without questioning the output of the mark-recapture analyses. Karanth (1995) was the first to use photographic data of tigers in combination with mark-recapture analysis. This was a pilot study and had no other purpose than to show that the analysis generated realistic estimates. Some studies merely showed that similar analyses were possible with other identifiable species as was the case with Henschel & Ray (2003) for leopards. Subsequent studies used Karanth (1995) as a template and began using the generated density estimates as comparisons between areas, for example between densities of tigers (Karanth & Nichols 1998, O'Brien et al. 2003, Kawanishi & Sunquist 2004) and between densities of jaguars (Silver et al. 2004, Maffei et al. 2004, Miller & Miller 2005, Miller 2005). Some of the studies examined relations between tiger densities and measures of prey density (Karanth & Nichols 1998, O'Brien et al. 2003), another compared densities of sympatric species, like jaguars and ocelots (Maffei et al. 2005). None of the camera studies explored the reliability or validity of the method to accurately and precisely enumerate population abundance and density.

The two most important assumptions for the use of mark-recapture analysis are that every individual in the study area has a catchability $> 0$ and that the estimated population is geographically and demographically closed (White et al. 1982). This study will focus on the assumption of catchability. Many individuals with capture rates close to zero (low catchability) can give rise to unreliable abundance estimates. White et al. (1982) recommended that the overall catchability ($\hat{p}$) of all captured individuals combined should be at least 0.1 or higher for reliable estimates, based on simulation studies (see Chapter 2). All the empirical studies cited above, except for the two tiger studies of (Karanth & Nichols 1998, Kawanishi & Sunquist 2004), failed to reach catchability of 0.1, with $0.02 < \hat{p} < 0.06$. The tiger studies of Karanth (1995) and Karanth & Nichols (1998) used multiple camera locations within an area that were shifted each day. This was possible because all cameras were accessible by vehicle. This potentially biases the sample to individuals that are willing to walk on large roads. If a subsection of the population avoids the larger roads they may have zero or low catchability. It is therefore important to understand the effect of low overall catchability, and the effect of heterogeneity in catchability in which a few members of the population have a lower catchability.

Many camera trap studies of individually recognisable species, like jaguars and tigers, are planned or in progress. Not all these studies will reach, scientific publication but they will be used in NGO reports, which will be used to shape policy. It is therefore necessary to validate the method and test its reliability. The reliability of the method depends on adequate sample sizes of individuals and re-captures (White et al. 1982, Menkens & Anderson 1988). The catchability of the surveyed population must be above a certain threshold to adequately sample the true population. Mark-recapture methodology was designed to estimate the size of populations that are uncountable because they are so large, such as insects, fish, birds, small mammals (Krebs 1994). Textbook discussions of mark-recapture techniques use examples of true population sizes of > 1000 (Krebs 1994, White et al. 1982). In contrast the use of mark-recapture techniques for camera trapping is not driven by sampling of large populations, rather it is driven by the elusive nature of the species - they are simply too difficult to count. A hypothetical futuristic method of satellite thermal imagery which detects all jaguars in an area would make mark-recapture obsolete since such an image would allow accurate counting due to low numbers. Without such futuristic methods, data are needed on the reliability of mark-recapture methods to estimate low populations with relatively low catchability. Accurate guidelines need to be produced which can inform a researcher whether or not the overall catchability ( $\hat{p}$ ) of the sample of their study population is sufficient to reliably estimate the population size. The guidelines should include the influence of heterogeneous catchability on abundance estimates (particularly the presence of high numbers of individuals with low individual catchability). Extreme levels of heterogeneity combined with generally low capture rates can be the main source of unreliability in estimates (Menkens & Anderson 1988). Abundance estimates have to be treated with extreme caution if the overall catchability and heterogeneity of catchability fall outside of the limits.

The simulations to investigate the effect of catchability conducted by White et al. (1982) were based on large populations with a relatively high number of individuals captured and relatively few capture occasions (trap days in live trapping). Mark-recapture analysis using camera trap data are rather the opposite; relatively few captured individuals with a relatively large number of capture occasions. Menkens & Anderson (1988), McKelvey & Pearson (2001) explored the effects of low catchability on model selection but their range of catchability did not reach the low levels of some of the camera trap studies discussed here. In this study simulations of mark-recapture studies were carried out using the low population size of 50 individuals with high numbers of trap occasions. The true population of 50 was estimated using varying rates of low catchability ( $\hat{p}$ ) and the level of discrepancies were noted between the true and the estimated population. This will give vital information of the catchability threshold level for estimating low density, cryptic populations.

It is difficult to assess the reliability of a single mark-recapture study without validation with an alternative method. Several years of data collected during this study provide the opportunity to indirectly test the reliability of the method. This is the first study with camera trap data from the same location with more than 2 consecutive years of data. No major changes, in terms of climate or prey numbers, occurred in the study area during this period that would explain significant increases or decreases in jaguar population. Any real population changes occurring over the course of the study are expected to be minor and the confidence intervals of population estimates are expected to show a high level of overlap between years. This study provides the first opportunity to examine the consistency of the estimates of mark-recapture analyses using camera trap data over time. Failure to find consistency in the present study will cast doubt on the reliability of the current method and should encourage researchers to collect additional data to demonstrate the reliability of their mark-recapture abundance estimates. Maffei et al. (2004) resurveyed two areas in Bolivia within a year. The density estimates of jaguars were similar between the periods despite changes in camera locations and length of survey. In contrast, Miller & Miller 2005 and Miller 2005 found no consistency in estimated jaguar abundance between 2004 and 2005 at their study site in Northern Belize.

In Chapter 2 it was concluded that the general survey length of large felid mark-recapture studies should not exceed 2-3 months and distances between camera traps should be based on the smallest home range of the target species (Karanth et al. 2002). Within these limits, abundance estimates should be robust with changes in survey length or camera location. Abundance estimates that are not robust in this way are useless since there is no way of knowing if the optimal survey length and spatial grid was used for sampling. The multiple years of data give the perfect opportunity to test the robustness of methodology. Sub-sampling of the data is to assess the effects of survey length on abundance estimates. Sub-sampling of different camera locations is used to assess the effects of spatial distribution of camera traps on abundance estimates. Lack of robustness in the present study would demonstrate that more attention needs to be given to the selection of suitable camera locations and/or to the optimal survey length.

The objectives of this chapter are:

1) To investigate the boundaries of reliability for mark-recapture analysis of camera trap data using simulation studies to estimate abundance for populations with a low heterogeneous catchability.
2) To investigate the consistency of abundance and density estimates for repeated camera trap surveys.
3) To investigate the robustness of camera trap data in terms of survey length and camera location by re-sampling the repeated survey data.

# Methods

## *Simulation studies*

Several simulations were run using the program CAPTURE in a similar manner as for White et al. (1982). The main aim of the simulations was to assess the level of deviation between estimated population size and the preset low population size of 50 individuals with varying low levels of catchability (low $\hat{p}$ values). All simulations were run using 30 and 60 occasions (equivalent of trap nights in live trapping). In this chapter, 'occasion' refers to a sampling point in time for presence-absence of individuals across camera traps. An 'occasion unit' refers to the unit of time over which the camera trap was left open to log a capture. For example, in Fig. 2.3 of Chapter 2, each of the 59 columns is an occasion, and the occasion unit is 1 day. 500 repetitions were run per simulation. The Jackknife estimator was used for all the simulations (the estimator most commonly used for camera trap studies of large cats, see Chapter 2).

CAPTURE created a simulated capture matrix of zeros and ones based on the predetermined catchability $\hat{p}$ . Each of the 50 individuals were randomly assigned ones and zeros based on the given $\hat{p}$ value for each occasion (30 or 60), creating matrices for which some individuals had trapping records and others not.

### 1. Simulations of varying $\hat{p}$ values

Fifteen simulations were run, starting with $\hat{p} = 0.01$ with increments of 0.01 up to $\hat{p} = 0.15$. No heterogeneity was set for this study meaning that all 50 individuals had the same capture chance. Each run produced a mean abundance estimate, and the average of the mean abundance for the 500 runs for each $\hat{p}$ value was calculated with 95% confidence intervals ($\pm 1.96 \times$ s.e.). The 15 average mean abundance estimates with confidence intervals were plotted in one figure for comparison.

For each $\hat{p}$ value (0.01 to 0.15) the percentage was calculated of the 500 runs that did not include 50 (the true population size) within the estimate's confidence intervals (percentage failure). A single run was equivalent to a single survey.

## 2. Simulations of varying $\hat{p}$ values with population structure

In the second simulation study, the effects of capture heterogeneity were explored using two different values of $\hat{p}$ to simulate heterogeneity. A population of 50 individuals was divided into two groups, each with their own $\hat{p}$ value: $\hat{p}_1$ and $\hat{p}_2$. The failure rate, calculated as above, was explored across two dimensions of heterogeneity of capture.

The first dimension concerned the level of heterogeneity in terms of the difference between $\hat{p}_1$ and $\hat{p}_2$. All combinations of the following values were used: $\hat{p}_1 = \{0.01, 0.02, 0.03\}$ and $\hat{p}_2 = \{0.05, 0.06, 0.07, 0.1\}$, creating 12 different levels of heterogeneity. The lowest level of $\hat{p}_1 = 0.01$ was considered a realistic minimum since this capture rate was equivalent to one capture in 3 months, which was observed for certain individual jaguars.

The second dimension concerned the number of individuals that were assigned to $\hat{p}_1$ and $\hat{p}_2$, starting with 49 individuals assigned a $\hat{p}_2$ value and one individual was assigned a $\hat{p}_1$ value. For each successive simulation one individual with a $\hat{p}_2$ value was assigned a $\hat{p}_1$ value until the population was equally divided with 25 individuals assigned a $\hat{p}_2$ value and 25 individuals assigned a $\hat{p}_1$ value.

In total, 25 simulations of 500 runs each were run for each of the 12 levels of heterogeneity (using both 30 occasions and 60 occasions).

## Abundance and density estimates

The intricacies of estimating abundance and density were discussed in Chapter 2. This chapter presents the results of abundance and density estimates for the 4 years of actual survey data. High levels of overlap between the 4 years would indicate consistency in estimates and would give indirect proof of the reliability of the mark-recapture method for camera trapping. The Jackknife estimator was selected as the best estimator fitting the data for all estimates in this chapter (see chapter 2 for Jackknife estimator).

Densities were calculated using two different procedures to compute the effective sampling areas (see Chapter 2 for meanings of effective sampling area and mean maximum distance moved, MMDM): The first procedure calculated the effective sampling area based on the MMDM for each year separately, based only on the movement data for the individuals captured in that particular year. The second procedure calculated the effective sampling area based on the average MMDM calculated across the 4 years. Densities were compared using the two different procedures of calculating the effective sampling area.

## Re-sampling of empirical data

The survey data were re-sampled to shorten survey length and to simulate the absence of certain cameras. The data subsets were used to estimate abundance and density using the program CAPTURE. Consistency in abundance and density estimates would indicate that the mark-recapture methodology is robust against variation in survey length and camera location.

### Comparison of surveys with constant location and duration

The influence of length of survey and location of camera, on abundance estimates were studied by keeping duration and location constant or variable for the four surveys. Duration was made constant between surveys (equal length of time) by reducing the number of days (occasions) for the surveys to the shortest survey (59 days). Location was made constant by excluding data from camera stations for which location varied between years (see Chapter 2 for details on variability of camera station locations).

Four sets of four abundance estimates were calculated using the program CAPTURE and compared for consistency between the 4 years: 1. The estimates with full survey length and all cameras present (original survey). 2. The estimates with length of survey constant (59 days) but all cameras included (time constant). 3. The estimates for the full survey length with only camera location included for those that were in similar locations (location constant). 4. The estimates with both length of survey and camera locations constant (both time and location constant).

### Re-sampling data for temporal analysis (reduction in days)

The influence of length of survey in each of the 4 years was studied further by eliminating successive days from the survey data and estimating abundance. This process was repeated until there were no longer enough individuals in the matrix to generate an estimate or there were simply no recaptures. It was expected that confidence intervals would be larger and the mean abundance more variable with increased reduction in number of days (occasions).

It was further explored whether any simple relation existed between mean abundance estimates and $\hat{p}$ values, number of individuals in the matrix and number of captures. The 4 years of data were pooled for this analysis. Relations per year were studied but only shown here if they differed from the pooled results.

### Re-sampling data for temporal analysis (comparison of survey halves)

To evaluate consistency within surveys over time, surveys were split into two halves of equal survey length. Abundance estimates using the program CAPTURE were compared for these two separate halves and for the full abundance survey. If the two independent survey halves gave the same abundance estimates and overlap in confidence intervals than this indicated that surveys were internally consistent across time.

### Re-sampling data for temporal analysis (choice of occasion unit)

Survey ‘occasion units’ were set as single days (see Chapter 2). In live trapping, trapping occasion is fixed because of the nature of trapping live animals (the checking regime dictates the trapping occasions). Camera traps were able to make new photographs immediately after recharging the flash. In theory a trapping occasion could be based on this short recharge time. The arbitrary choice of 24 hours for camera trapping was based on one full day's cycle of activity in the life of a jaguar but more days can be included as a unit by grouping several days together into a new unit of trap occasion.

The effects of different grouping regimes were studied from single day occasions (original survey unit) up to a week as one occasion (seven 24-hour periods grouped together). Program CAPTURE was used to calculate abundance per survey for the seven different occasion units (1 day to 1 week). Increases in precision with grouping were judged from the size of the confidence intervals.

Any capture within the grouped days resulted in a capture for the new unit occasion (for example the grouping of 2 days into one new occasion was: 00 = 0, 01 = 1, 10 = 1, 11 = 1). The effects of grouping on $\hat{p}$ values were studied by plotting $\hat{p}$ values against number of days used as occasions. The original number of days did not allow complete partitioning into the different occasion units. The "leftover" days were added as a single occasion regardless what the number of days to ensure that no captures were excluded from the analysis.

## Re-sampling for spatial analysis

Three areas could be distinguished within the main survey of the CBWS, which the jaguars seemed to use as discrete units. There was only minor overlap of individuals captured between these areas (see Chapter 5 for geographic variation of individual jaguars). The minimal exchange between them meant that they could be analysed as spatially discrete units. The three areas were: the "Sale Si Puede" trail area ("SSP", 5 cameras), the "Victoria Peak" trail area combined with the upper parts of the "Mexican Branch" area ("Vic", 6 cameras) and the "Western trail" area ("West", 6 cameras). The results for "West" were split into two separate estimates, one with and one without camera station 20. Camera 20 was at the edge of the survey located on the entrance road into CBWS. This road is used by many animals to cross the surrounding ridge. The camera seemed to be on the boundary between two geographically distinct areas. For this reason, abundance was estimated results for "West" with and without this camera station.

Figure 3.1 shows that the area of the three units differed, so comparisons were made between density estimates rather than between abundance estimates. For each survey year density was only calculated if the full set of cameras within the area were functioning (See Chapter 2 for estimation of density). Density estimates were compared between the three units and within each unit between the years.

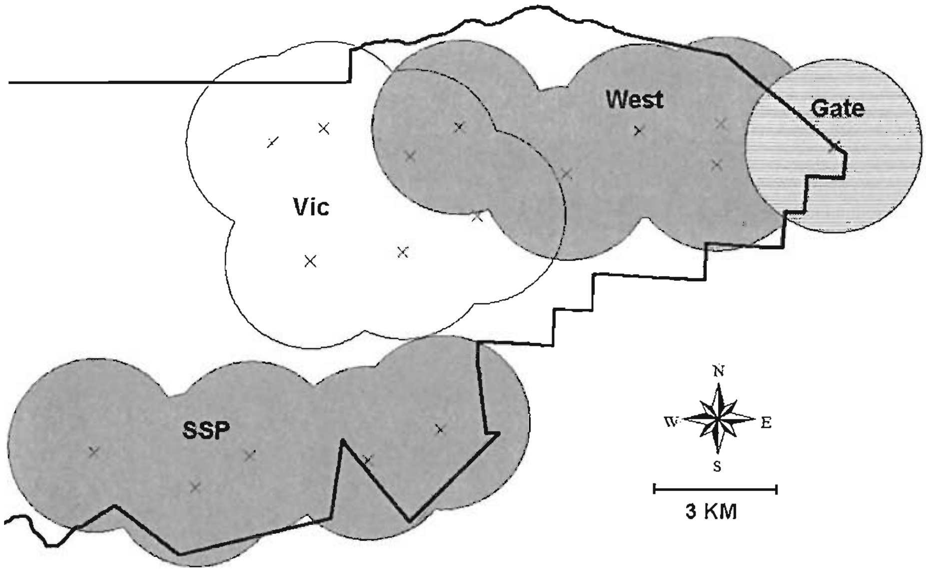

Figure 3.1. The three areas derived from the main surveys: Sale Si Puede area (SSP, grey), Victoria Peak area (Vic, white) and Western trail area (West, grey). All camera locations are marked with an X. The circular areas surrounding each camera station are the buffer strips with a radius of 2.36 km making up the effective sampling area for each of the three areas. The cross-shaded circle is the buffers strip surrounding the camera station 20 at the gate of the park.

## Results

### 1. Simulations of varying $\hat{p}$ values

All 15 confidence intervals, for both sets of trials included the abundance estimate 50 within their range (Figure 3.2). The 60-occasion simulations showed relative high precision around $\hat{p} = 0.05$, while this was reached at $\hat{p} = 0.07$ for 30-occasion simulations. Figure 3.2 shows that the range of means for $\hat{p} > 0.09$ showed a narrow distribution of means, converging to 50 after $\hat{p} > 0.02$ for the 60 occasions, while the 30 occasions still had substantial variation up to $\hat{p} = 0.15$ and continuous slight overestimation for $\hat{p} > 0.02$.

Figure 3.3 shows that the percentage failure for 30 occasions increased dramatically when $\hat{p} < 0.04$. The percentage of failures in this region of $\hat{p}$ values was too high (above 5%) to make single run estimates, equivalent to a single survey, trustworthy. For 60 occasions only $\hat{p} = 0.01$ had a failure rate that was too high to trust estimates of a single run. Both datasets showed a small increase in failure for higher $\hat{p}$ values, for 30 occasions around $\hat{p} = 0.11$ and for 60 occasions around $\hat{p} = 0.06$, which went down again after $\hat{p} = 0.11$ (a small peak). The average standard error surrounding the individual means (s.e. per run) dropped dramatically for the $\hat{p}$ values in this range which might have caused the slight increase of failure. The precision increased here but the accuracy was not high enough to include the true population value. Reliable estimates were generated for $\hat{p} < 0.01\text{-}0.04$ but accuracy and precision of the mean abundance estimate required $\hat{p} < 0.05\text{-}0.07$.

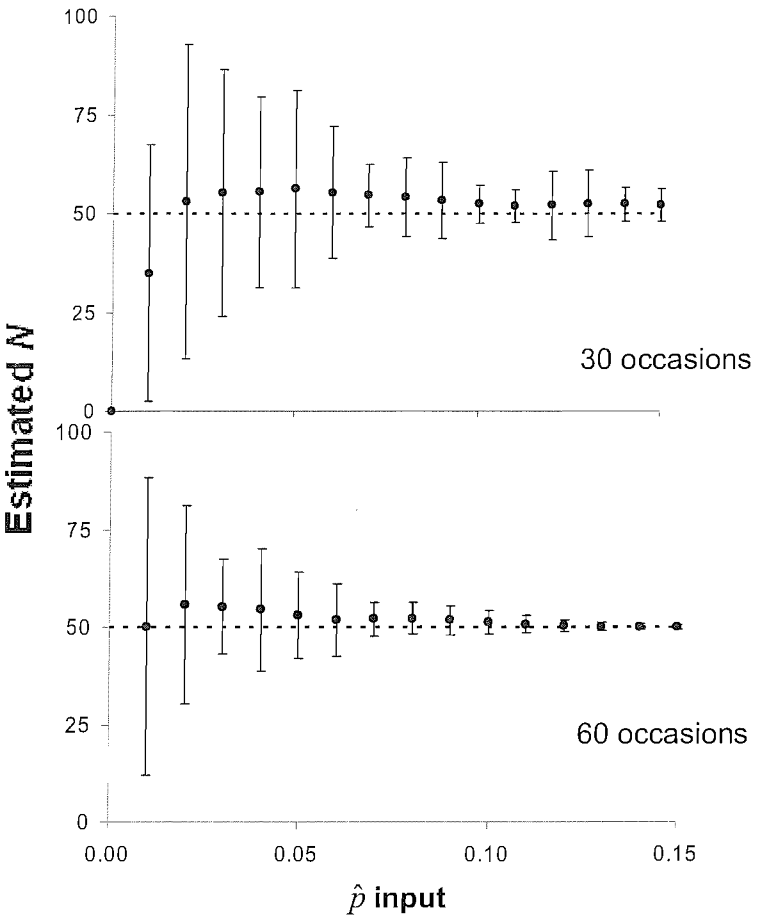

Figure 3.2. Abundance estimates with 95% confidence intervals for different $\hat{p}$ values for a population with a true population size of 50 (upper panel results 30 occasions, lower panel results 60 occasions).

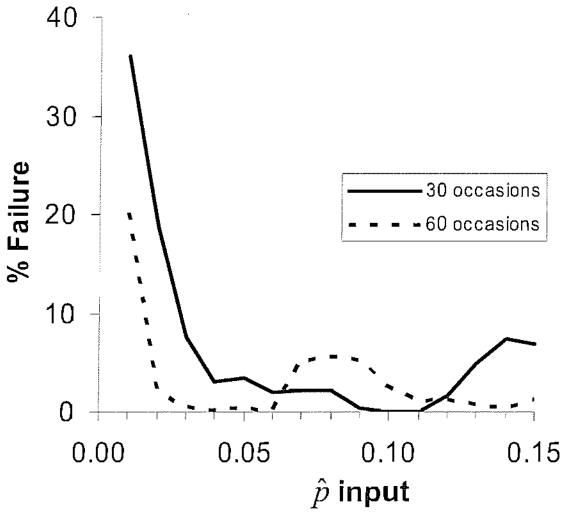

Figure 3.3. The percentage of runs per simulation that did not include $N = 50$ within confidence intervals, for simulations with 30 and 60 occasions. Based on 500 runs per simulation.

## 2. Simulations of varying $\hat{p}$ values with population structure

Several inferences can be drawn about the effects of heterogeneity from Figure 3.4:

1) Intuitively it was expected that higher $\hat{p}$ values would always contribute to a higher reliability. The results show that the higher the value of $\hat{p}_2$, the higher the failure rate. This result could be interpreted in terms of the difference between $\hat{p}_1$ and $\hat{p}_2$. In effect, the higher the level of heterogeneity, larger differences between the $\hat{p}_1$ and $\hat{p}_2$, the higher the failure rate. The more similar the values of $\hat{p}$ were for a population the lower the failure rate.

2) The percentage failure increased as $\hat{p}_1$ decreased. This effect was consistent with Figure 3.3. The slope of the increasing failures became shallower when $\hat{p}_1$ was increased from 0.01 to 0.03.

3) Effects of heterogeneity were only evident when a substantial percentage of the population had low $\hat{p}_1$ values, regardless of the $\hat{p}_2$ value. This occurred when ≥12% of the population had $\hat{p}_1 = 0.01$; or ~ 16% of the population had $\hat{p}_1 = 0.02$ ;or 22% of the population had $\hat{p}_1 = 0.03$ (failure was low throughout for this $\hat{p}_1$ value).

4) Simulations using 60 occasions had a lower percentage failure than those using 30 occasions. The longer the sampling period (number of occasions) the greater chance that individuals with low catchability were detected, lowering the failure rate and increasing accuracy. For 30-occasion trials, the failure rate was low ( < 5%) when $\hat{p}_1 > 0.02$ for all levels of heterogeneity and all values of $\hat{p}_2$. For 60-occasion trials, $\hat{p}_1$ could fall to > 0.01 before the same failure rate was reached.

5) The conclusion in point 3 above noted that effects of heterogeneity were only noticeable after a substantial percentage of the population had low $\hat{p}_1$ values. This was true for all the trials except for the three trials with 60 occasions and $\hat{p}_2 = 0.1$. Here a small failure peak was noted right at the start, with only a small percentage of the population having $\hat{p}_1$ values (peaks in the graphs with failure at 10%-14%). The average s.e. was small within ranges with these peaks compared to the same ranges of the other trials without them. This meant that the precision was high but the accuracy generally not high enough to include the true population size in this region for a large percentage of the runs.

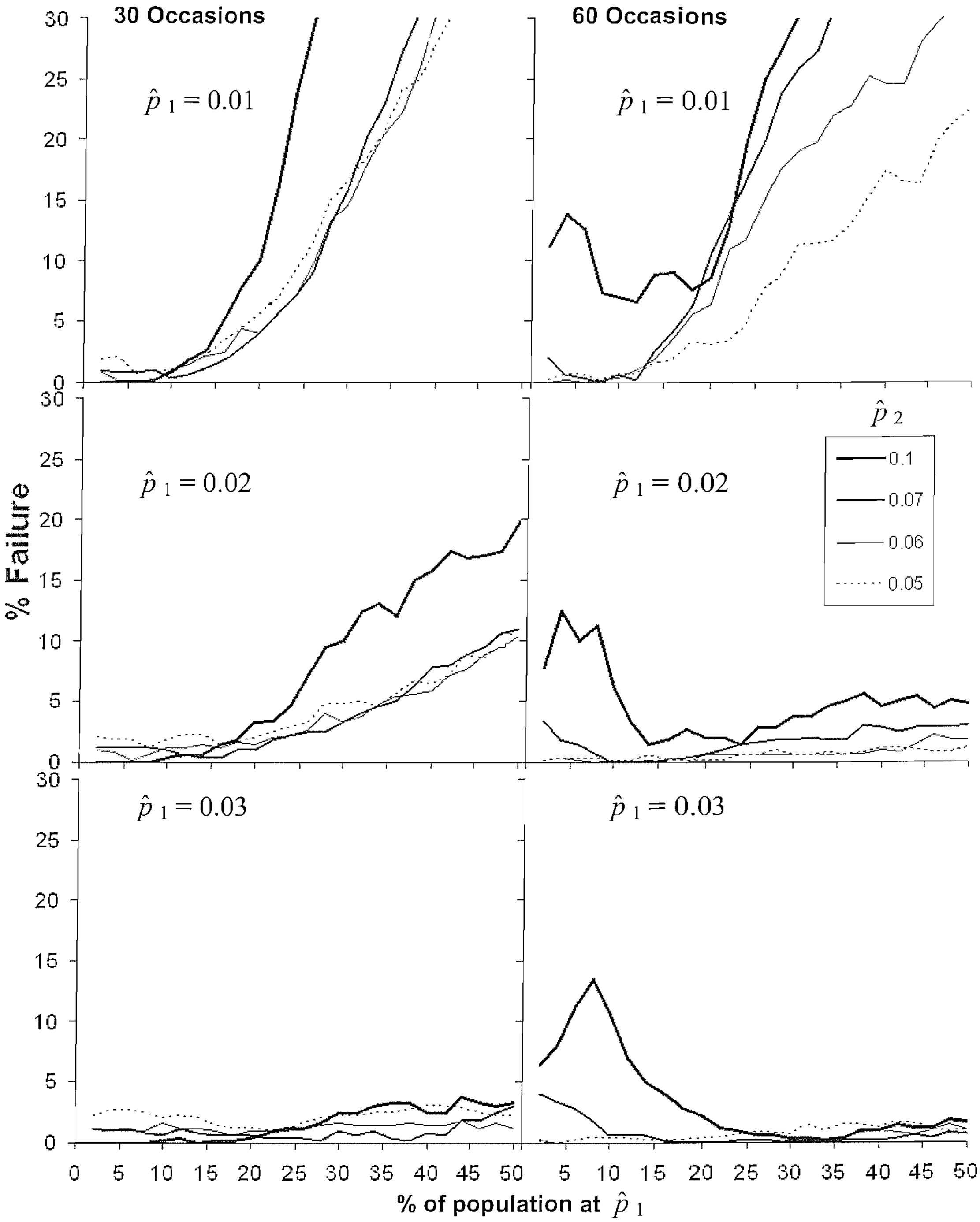

Figure 3.4 The percentage of runs per simulation that did not include $N = 50$ within confidence intervals (% Failure). The population of 50 was divided into two different catchability coefficients ($\hat{p}_1$ and $\hat{p}_2$). Twelve different $\hat{p}_1$ and $\hat{p}_2$ combinations were used for two sets of occasions (left side = 30 occasions, right side = 60 occasions). $\hat{p}_1$ is kept constant per panel and $\hat{p}_2$ varied as shown in the legend.

## *Abundance estimates*

Table 3.1 shows the abundance estimates for the four actual surveys. The null hypothesis for the closure test was not rejected, meaning that all surveys had a statistically closed population (the captures were evenly spread across the survey period, see Chapter 2 for explanation of closure test). The overall catchability values ($\hat{p}$) were low for all the surveys, with 2003 having the highest $\hat{p}$ and the smallest confidence intervals. The $\hat{p}$ value of the year 2004 was below 0.03 which could indicate unreliability of the estimate.

There is a striking difference between the four surveys in number of individuals photographed (9 to 20) and the number of capture events (37 to 80). In particular, 2004 had a high number of capture events, with eight individuals being photographed at a single camera location (camera 20). The survey period was longer in 2004 and 2005, compared to 2002 and 2003, and likely contributed to the greater number of individuals and capture events in these years.

Table 3.1 Abundance estimates of jaguars using the program CAPTURE for the four main surveys together with the total number of individuals photographed and total number of captures (photographic events).

| Year | Survey days | Total *N* individuals (Total *N* captures) | Closure test Z value (p-value) | $\hat{p}$ | Abundance Ab. (± s.e.) | 95% CI Range |
|---|---|---|---|---|---|---|
| **2002** | 59 | 11 (37) | -0.94 (0.17) | 0.04 | 14 (±3.57) | 12-30 |
| **2003** | 65 | 9 (40) | 0.81 (0.79) | 0.06 | 10 (±1.53) | 10-17 |
| **2004** | 72 | 20 (80) | 0.53 (0.70) | 0.03 | 35 (±9.17) | 25-65 |
| **2005** | 77 | 20 (64) | 0.14 (0.56) | 0.04 | 21 (±9.72) | 21-85 |

Figure 3.5 displays the abundance estimates with confidence intervals for the 4 years. The only substantial overlap in confidence intervals between years was 2003 with 2002 and 2005 with 2004, suggesting sampling error between years. Particularly the year 2003 fell below the levels of the other 3 years. There seemed to be a large difference between the years 2002/2003 and the years 2004/2005, the mean increases three-fold between 2003 and 2004. The year 2004 had the lowest $\hat{p}$ value (0.03), potentially causing overestimation of abundance compared to the highest $\hat{p}$ value for 2003 (0.06). The range of 2005 ($\hat{p}$ = 0.04) still did not overlap with the range of 2003.

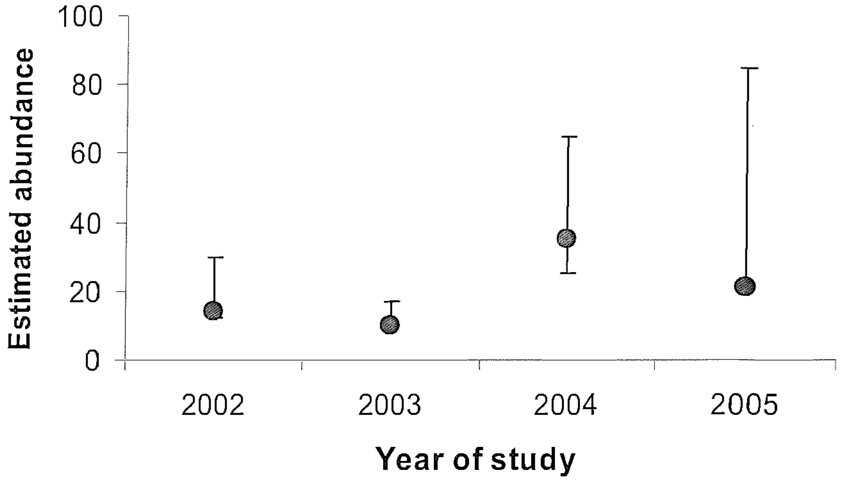

Figure 3.5 Jaguar abundance estimates and 95% confidence intervals, obtained from the program CAPTURE for the four main surveys.

## *Density estimates*

The parameters for estimating density were calculated for each of the four surveys (mean maximum distance moved (MMDM), buffer strip width and effective sampling area, see Chapter 2). Table 3.2 shows that there was variation between the 4 years in the MMDM hence the estimated buffer strip width and the effective area. In the 2002 survey the buffer strip width was low with a large s.e. due to a few individuals moving widely whilst the majority of individuals did not move far. Effective sampling area was also influenced by camera removal but the 2003 survey had the largest effective area due to the large MMDM. The density estimates vary substantially between the surveys with a similar large difference between the 2003 and 2004 estimates, as was found for the abundance estimates (Figure 3.5).

Table 3.2. Densities calculated for each survey year. The effective area was calculated each year, based on the mean maximum distance per year. The density was calculated using abundance estimates in Table 3.1.

| Year | Mean max. dist. *d* in km | Buffer strip *W* ± (s.e.) in km | Effective area *A (W)* ± (s.e.) in $km^2$ | Density *D* (± s.e.) ind per $100km^2$ |
|---|---|---|---|---|
| **2002** | 3.89 | 1.95 (±1.18) | 159.20 (±52.93) | 8.80 (±3.69) |
| **2003** | 5.62 | 2.81 (±0.52) | 207.50 (±26.56) | 4.82 (±0.96) |
| **2004** | 4.79 | 2.39 (±0.44) | 191.40 (±21.49) | 18.29 (±5.21) |
| **2005** | 4.59 | 2.29 (±0.54) | 183.37 (±25.97) | 11.45 (±5.54) |
| Average | 4.72 | 2.36 (±0.67) | 189.15 (±31.74) | 10.84 (±3.85) |

In Table 3.3 the MMDM averaged over the four surveys was used to estimate density for each of the surveys. The width of the buffer strip was therefore kept constant for all surveys and the area of the survey depended only on the number of camera locations (this differed for each survey as explained in Chapter 2). Table 3.3 shows that the density estimates based on an averaged MMDM were higher than those based on survey-specific MDMM Table 3.2.

Table 3.3. Densities calculated for each survey year. The effective area was calculated each year, based on the average mean maximum distance for all the years. The density was calculated using abundance estimates in Table 3.1.

| Year | Mean max. dist. *d* in km | Buffer strip *W* ± (s.e.) in km | Effective area *A (W)* ± (s.e.) in $km^2$ | Density *D* (± s.e.) ind per $100km^2$ |
|---|---|---|---|---|
| **2002** | 4.72 | 2.36 (±0.67) | 194.14 (±36.26) | 7.21 (±2.28) |
| **2003** | 4.72 | 2.36 (±0.67) | 171.81 (±34.11) | 5.82 (±1.46) |
| **2004** | 4.72 | 2.36 (±0.67) | 189.15 (±35.79) | 18.50 (±5.98) |
| **2005** | 4.72 | 2.36 (±0.67) | 189.15 (±35.79) | 11.10 (±5.55) |

Figure 3.6 shows the density estimates based on Tables 3.3 and 3.4. There was no complete overlap in the 95% confidence range of density for all four surveys for the original calculations (MMDM calculated per year) with the estimates of 2003 not overlapping with those of 2004. There was overlap in density using the average MMDM. The size of the 95% confidence intervals increased for the years 2003 and 2004 using the average MMDM, causing the two ranges to overlap slightly. The confidence intervals for both density estimates of 2004 and 2005 were extremely large.

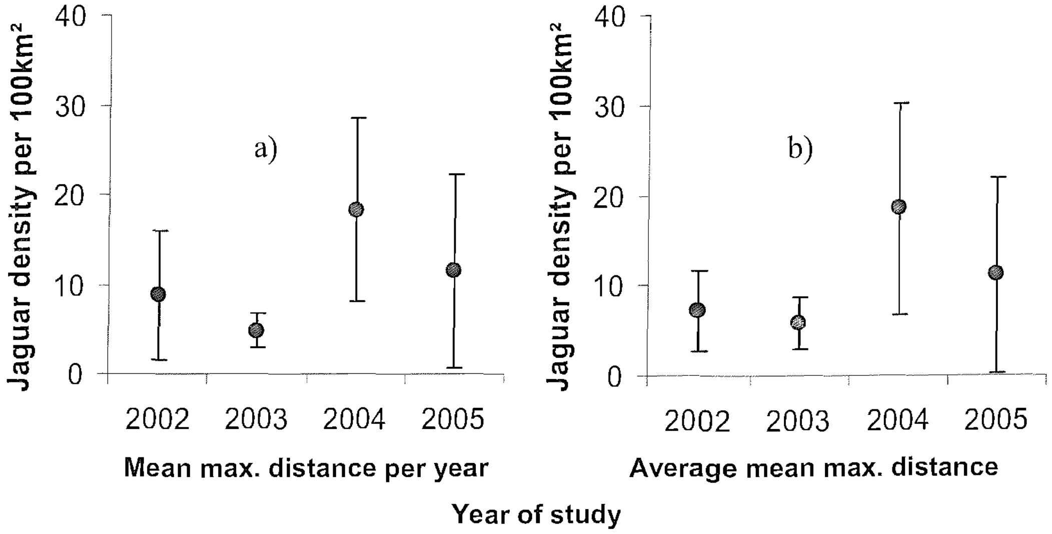

Figure 3.6 Density estimates with 95% confidence intervals for the 4 years of surveys based on two procedures to calculate the mean maximum distance. a) based on the mean maximum distance calculated per survey (see Table 3.2). b) based on the average mean maximum distance calculated over 4 years (see Table 3.3).

## *Comparison of surveys in time and space*

The four main surveys differed in length and in some camera locations. Abundances were estimated from three subsets of data: 1) constant survey length 2) constant survey location 3) constant survey length and location and compared with the original main survey data. The closure test was not significant for any of the datasets, meaning that the capture records were evenly distributed across the survey period, indicating statistical closure.

Table 3.4 shows that the overall catchability ( $\hat{p}$ ) were least variable when survey length was constant. If survey length was fixed, individuals with single or few captures had the same individual catchability between surveys, causing convergence of the overall $\hat{p}$ values.

Table 3.4 The $\hat{p}$ values as estimated by the program CAPTURE for the four types of survey manipulations for each year: Original survey (All), survey length is constant (Time), survey location is constant (Space) and survey length and location are constant (Full).

| | $\hat{p}$ value | | | |
|---|---|---|---|---|
| **Year** | **All** | **Time** | **Space** | **Full** |
| **2002** | 0.04 | 0.04 | 0.05 | 0.05 |
| **2003** | 0.06 | 0.05 | 0.06 | 0.04 |
| **2004** | 0.03 | 0.04 | 0.04 | 0.03 |
| **2005** | 0.04 | 0.04 | 0.03 | 0.03 |

Abundance estimates, based on data from survey that were standardised in time and/or space were more similar across the years than the original survey data (Figure 3.7). Estimates for which both survey length and location were constant ("Full") presented an acceptable result for abundance estimates in terms of similarity across the years. Variation in camera location was a greater cause of variability in abundance estimates than was survey length. These results show that it is important to focus efforts on improving choice of camera deployment rather than extending the length of surveys to improve accuracy.

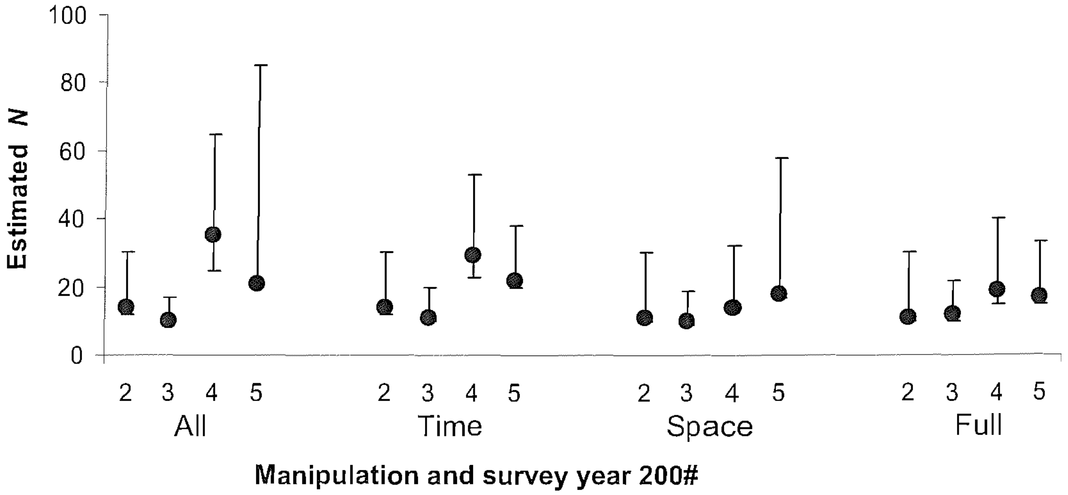

Figure 3.7. The abundance estimates with 95% confidence intervals for the 4 years of survey data. "All" = complete data set; "time" = constant survey length, "space"= constant survey location, "full" = constant survey length and location.

## *Temporal variation studies*

### Elimination of days

It was expected that as days were removed from the capture matrix, the estimates would become less reliable and the confidence intervals larger with unreliable mean abundances. The pattern shown in Figure 3.8 was far more erratic than expected. The confidence intervals for the 2005 estimates showed a marked reduction after the removal of 6 days and the abundance estimates and confidence intervals for the 2004 survey increased between the removal of the 6th and 11th day. In effect the 2004 abundance estimates would have been quite different if the survey had been just 6 days shorter than its full length, which fell well into the length of the other surveys. The results showed that abundance estimates could fluctuate greatly with number of occasions, even with number of occasions that fell well within the range for regular surveys.

The fluctuations can be explained in terms of the low ratio of absence to presence in the capture matrix (ratio absence:presence, 2002 = 37:649, 2003 = 40:585, 2004 = 80:1440, 2005 = 64:1540). Removal of survey days will on average remove more "absence" than "presence" so increasing the overall catchability $\hat{p}$. The $\hat{p}$ values show sudden crashes when recaptures were removed from the matrix and sudden jumps when captures were removed from the matrix of individuals with only a single capture (see next section). The removal of a single capture individual from the matrix meant that the entire row of "absences" prior to this capture also disappeared, so increasing the overall catchability. This explains the large fluctuations in 2004, since there were relatively many single individuals within the matrix, with the captures unevenly spread across all the individuals. In contrast, the year 2005 had similar numbers of individuals captured as 2004 but the captures were more evenly spread across the individuals. The year 2003 also had its captures evenly spread across the individuals for the whole period but the first 20 days showed a more skewed distribution with a few individuals being captured at a higher rate than others, creating high fluctuations during the first part of the survey (between 28-41 days removed). The higher levels of heterogeneity in individual catchability caused inconsistencies in abundance estimates.

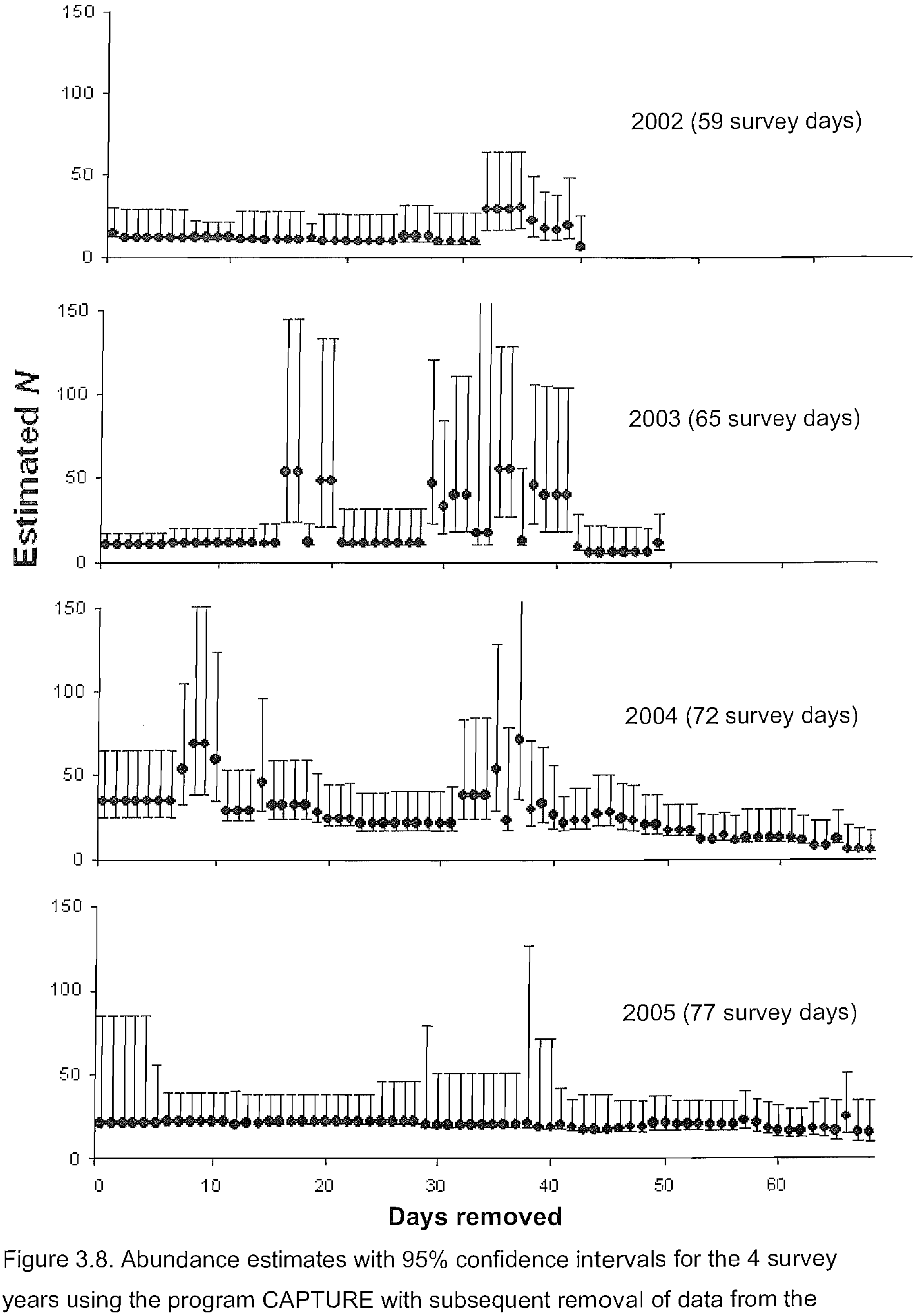

Figure 3.8. Abundance estimates with 95% confidence intervals for the 4 survey years using the program CAPTURE with subsequent removal of data from the capture matrix per day.

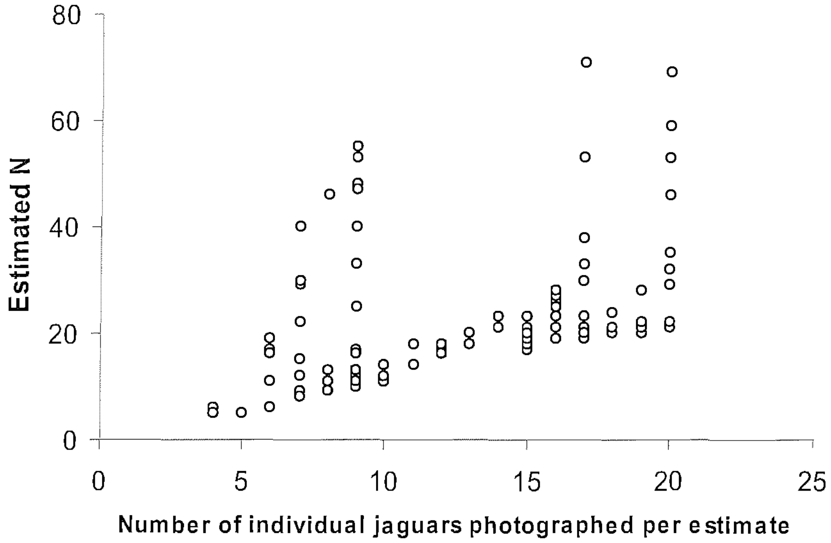

Figure 3.9a. Dependency of mean abundance estimates on number of individuals for the combined dataset of all years.

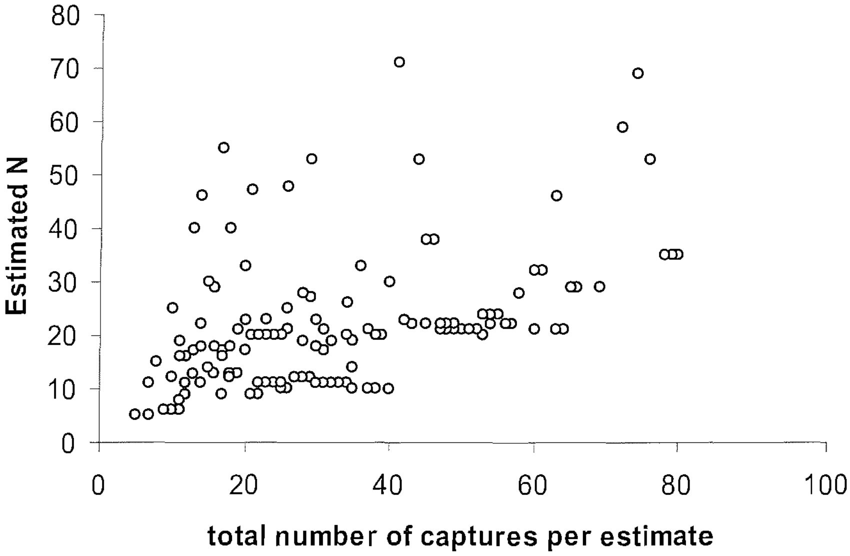

Figure 3.9b. Dependency of mean abundance estimates on number of captures for the combined dataset of all years.

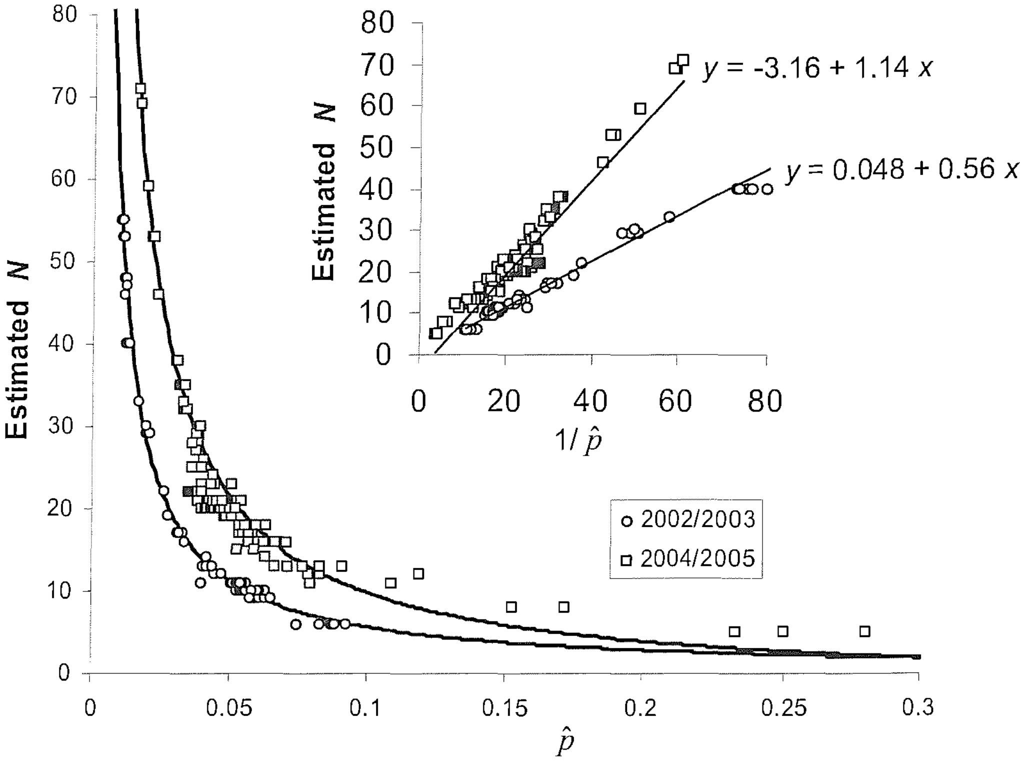

Figure 3.9c. Dependency of mean abundance estimates on $\hat{p}$ for the combined dataset of all years.

Figures 3.9a, b and c show the relations between the mean abundance estimates for the removal study and the associated number of individuals, total captures and $\hat{p}$ values. Figure 3.9a shows a weak positive relationship between the number of individuals captured and the estimated mean abundance based on four surveys. The regression of log10 ($N$) against the log10 number of individuals explained a small but significant percentage of the variation ($r^2 = 0.38, p < 0.01$). When partitioned by year the log10 number of individuals explained a large percentage of the variance in log10 ($N$), for the 2004 ($r^2 = 0.80$) and 2005 ($r^2 = 0.49$) surveys but not for the 2002 ($r^2 = 0.00$) and 2003 ($r^2 = 0.08$) surveys.

Figure 3.9b shows that there was also a weak positive relationship between number of captures and estimated mean abundance based on four surveys. Log10 number of captures explained less variation for abundance estimates than did log10 number of individuals ($r^2 = 0.25, p < 0.01$). When partitioned by year, only the log10 captures for the 2004 ($r^2 = 0.75$) and 2005 ($r^2 = 0.40$) surveys explained a substantial proportion in the variance of log10 ($N$), while log10 captures of the 2002 ($r^2 = 0.07$) and 2003 ($r^2 = 0.00$) surveys explained little variance in log10 ($N$). The number of individuals and the number of captures were highly correlated (Pearson correlation 0.85, $p < 0.01$ for log10 transformed data). These results suggested that neither the number of captures nor the number of individuals were sufficiently reliable predictors of mean abundance.

Figure 3.9c shows two inverse relations between the mean abundance estimate and $\hat{p}$, clearly distinct in terms of differences between years: the upper line represents data for the years 2004 and 2005 and the lower line for the years 2002 and 2003. Separate plots for each survey year (not shown here) showed the same inverse relation. Only the 2005 data had a limited range of the curve (see Figure 3.8). All the peaks in estimated abundance, as days were eliminated from the survey, (Figure 3.8) could be explained in terms of low $\hat{p}$ values. Figure 3.9c, along with Figure 3.3, suggested that reliable mean abundances were estimated for $\hat{p} > 0.05$. Lower $\hat{p}$ values resulted in an overestimation of abundance.

Mean abundance had a linear relation to $1/\hat{p}$ (inset Figure 3.9c), with strong predictive power ($r^2$ values of 0.99 and 0.90 for the two lines respectively). Analysis of covariance demonstrated a significant difference in the slopes (Table 3.5, year by $1/\hat{p}$ interaction).

Table 3.5 GLM for abundance estimate as response variable with $1/\hat{p}$ as a covariate and the years 2002/2003 and 2004/2005 as two categorical variables.

| **Source** | **d.f.** | **SS** | **MS** | ***F*-value** | ***p*-value** |
|---|---|---|---|---|---|
| $1/\hat{p}$ | 1 | 8.98 | 9.97 | 4110.14 | **0.00** |
| **Year** | 1 | 3.20 | 0.18 | 72.61 | **0.00** |
| **Year * 1/** $\hat{p}$ | 1 | 0.02 | 0.02 | 7.11 | **0.00** |
| **Error** | 225 | 0.55 | 0.00 | | |
| **Total** | 228 | 12.74 | | | |

The linear relation between estimated abundance and $1/\hat{p}$ (inset Figure 3.9c) meant that if $\hat{p} \rightarrow 0$ then the "estimated $N$"→ ∞, meaning extreme overestimation at low $\hat{p}$ values. The catchability $\hat{p}$ represents the average number of captures per trap occasion, meaning that $1/\hat{p}$ represents average number of occasions (days) between captures. When $1/\hat{p} \rightarrow 0$ (the time between captures approached zero, meaning that all cameras were constantly capturing jaguars), then the estimated $N \rightarrow$ true $N$. The point at which $1/\hat{p} \rightarrow 0$ is the intercept of the regression line with the $y$-axis (the value of the constant in the regression equation). On the main graph of Figure 3.9c this point represents the asymptote along the $x$-axis. In theory the constant in the regression equation should represent the true population size.

The shallower the slope of the regression lines for $1/\hat{p}$ (lower the multiplier for the $x$ value) the quicker the curves levels out to the asymptote value. The ideal line would be a straight horizontal line with the multiplier→0, meaning that each $\hat{p}$ value gives the same mean abundance equal to the constant. This shows that the present fitted curves would not reach an asymptote with the real abundance since the asymptote values of the constant in the regression equations were 0.048 and -3.16. The 2002/2003 curve appears more reliable than the 2004/2005 curve since it flattens out at a faster rate. The fit for the 2004/2005 curve was less for higher values of the $\hat{p}$ range in the tail of the curve. The real 2004/2005 data showed more levelling off for higher $\hat{p}$ values than the estimated curve, indicating higher reliability for the real data then the curve would suggest.

Regressions between mean abundance and $1/\hat{p}$ were calculated per year to compare slope and constants between years (Table 3.6). All years had a strong linear relation between mean abundance and $1/\hat{p}$. The grouping in Fig. 3.9c of 2002/2003 was warranted since relatively similar equations were found for the 2 years and the total equation of Figure 3.9c (inset). The equations for 2004 and 2005 differed substantially. The overlap in points was mainly caused by the small range of mean abundances of 2005, falling within data points of the much larger range of mean abundances of 2004. Table 3.6 shows that only the year 2005 had a realistic constant (9.3) and the shallowest slope (0.48). The value of 9 is roughly half of the mean estimate for 2005 as measured in the section of abundance measures (20 individuals were captured during this survey). A GLM analysis with $1/\hat{p}$ as a covariate and the 4 years as categorical variables was carried out to test if the four lines were significantly different from each other. Table 3.7 shows that the influence of $1/\hat{p}$ on abundance varied strongly between years.

The existence of the inverse relation for all the datasets means that overestimation for low $\hat{p}$ is a serious problem. The steeper the slope, the higher the threshold will be with high $\hat{p}$ values still giving overestimated abundance estimates. The present range of the data suggests that unreliability for $\hat{p} < 0.05$ should still be considered as a rule of thumb since it was shown that mean abundance was greatly overestimated within this region. The inverse relation should be further explored for other camera trap studies in other geographic regions to investigate the full extent of this relation. Especially from regions where the abundance estimates were considered more reliable.

Table 3.6 Regression analysis for the relation of mean abundance and $1/\hat{p}$ per year. Significant results ($p < 0.05$) are shown in bold.

| | | **Standard Error** | | |
|---|---|---|---|---|
| **Year** | **Equation** | **constant** | **coefficient** | $r^2$ |
| 2002 | $y = -0.92 + 0.60\,x$ | **0.25** | **0.01** | 0.99 |
| 2003 | $y = 0.19 + 0.56\,x$ | 0.19 | **0.01** | 0.99 |
| 2004 | $y = -1.98 + 1.18\,x$ | **0.48** | **0.02** | 0.99 |
| 2005 | $y = 9.31 + 0.48\,x$ | **0.73** | **0.03** | 0.77 |

Table 3.7 Table 3.5 GLM with abundance estimates as response variable, $1/\hat{p}$ as a covariate and the 4 years (2002, 2003, 2004 and 2005) as categorical variable.

| **All years** | **d.f.** | **Seq. SS** | **Adj. SS** | **Adj. MS** | ***F*-value** | ***p*-value** |
|---|---|---|---|---|---|---|
| **$1/\hat{p}$** | 1 | 25954.20 | 5674.90 | 5474.90 | 3012.84 | **0.00** |
| **Year** | 3 | 4713.50 | 214.90 | 71.60 | 38.03 | **0.00** |
| **Year * $1/\hat{p}$** | 3 | 3273.90 | 3273.90 | 1091.30 | 579.39 | **0.00** |
| **Error** | 221 | 416.30 | 416.30 | 1.90 | | |
| **Total** | 228 | 34357.90 | | | | |

### Comparison of periods within surveys

Each survey was divided into two equal time periods and the abundance estimated for each and compared with the complete survey. The null hypothesis of closure could not be rejected for any of the abundance estimates, indicating statistical closure. Figure 3.10 presents the estimates and 95% confidence intervals with corresponding $\hat{p}$ values below the distribution.

The estimated mean abundances were similar for both halves and the complete dataset and all confidence intervals showed a high degree of overlap. There were two anomalies in these results: 1. The 2004 complete survey had a mean abundance that differed substantially ( > 10) from its two halves but there was still substantial overlap in confidence intervals. 2. The abundance estimates based on the first half of the 2003 survey had extremely large confidence intervals compared to the other halves. Both estimates, complete survey 2004 and first half 2003, had $\hat{p} < 0.03$, which previous data showed could indicate that the data were unreliable and overestimated true abundance. The estimates based on the two halves of 2004 were probably closer to the true population abundance than estimates based on the complete 2004 dataset. Overall, the data in Figure 3.10 indicated that there was consistency between the survey halves and the total survey when $\hat{p}$ values were > 0.03. Despite the fluctuations in abundance estimates when days were removed from the survey (previous section), abundance estimates were consistent between two halves of the survey. This is important because estimates would be worthless if they changed depending on which period was sampled.

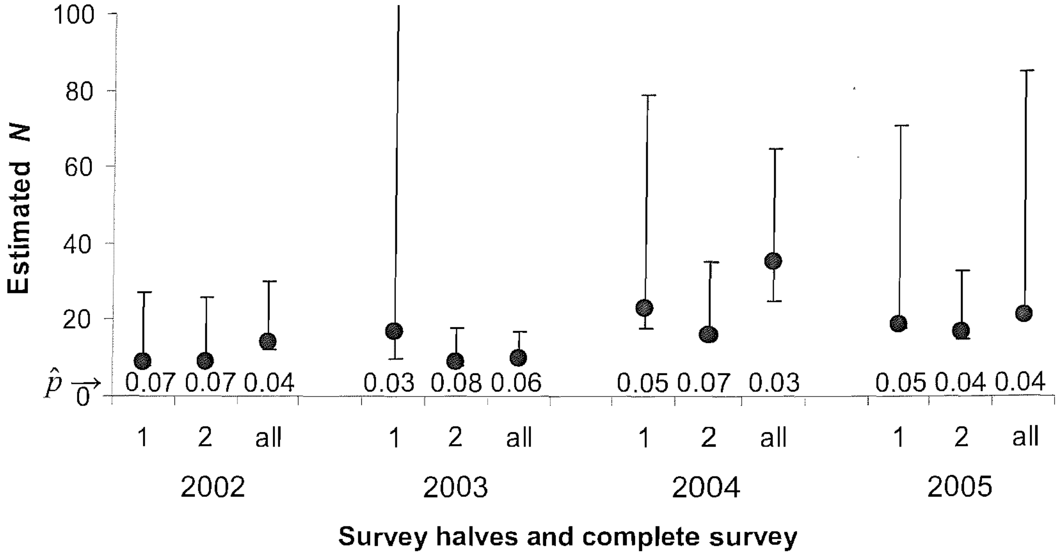

Figure 3.10. Abundance estimates using the program CAPTURE were estimated per year for two equal parts (1 and 2) of the survey and the complete survey.

## Variation in time units for each occasion

Table 3.8 shows that the number of occasions used in a capture matrix diminished exponentially with increased number of days grouped together to form a unit. The greatest reduction in number of occasions within the survey was made when an occasion was changed from a 1-day unit to 2-day unit.

Table 3.8. Number of days used as a unit in relation to the number of occasions used for the four surveys.

| | Number of days in unit | | | | | | |
|---|---|---|---|---|---|---|---|
| **Year** | **1** | **2** | **3** | **4** | **5** | **6** | **7** |
| **2002** | 59 | 30 | 20 | 15 | 12 | 10 | 9 |
| **2003** | 65 | 33 | 22 | 17 | 13 | 11 | 10 |
| **2004** | 72 | 36 | 24 | 18 | 15 | 12 | 11 |
| **2005** | 77 | 39 | 26 | 20 | 16 | 13 | 11 |

Figure 3.11 shows that the confidence intervals of the abundance estimates became narrower with increased occasion unit length. This was most pronounced for the 2004 and 2005 estimates. The 2003 survey was the exception; here the estimate based on 1-day occasions had the smallest confidence intervals. The $\hat{p}$ value shows a steady linear increase with increased occasion unit length (Figure 3.12). The generally high ratio of absence:presence for all the surveys (see section Elimination of days) meant that the grouping of data into longer occasion units reduced the number of absence occasions (no captures) more compared to the number of presence occasions (captures). This reduction in absence occasions caused an increase in $\hat{p}$. The 2003 survey had higher $\hat{p}$ values than the other surveys (Figure 3.12). Few individuals had many captures in short time intervals. Consequently when occasion length was increased there was a relatively greater reduction in “presence” occasions days compared to the other years, and so the estimates based on a 1-day occasion unit estimate was the most precise. The mean of the 2004 estimate dropped with the increase in occasion unit length indicating that the original estimate, based on 1-day occasion, was probably an overestimation.

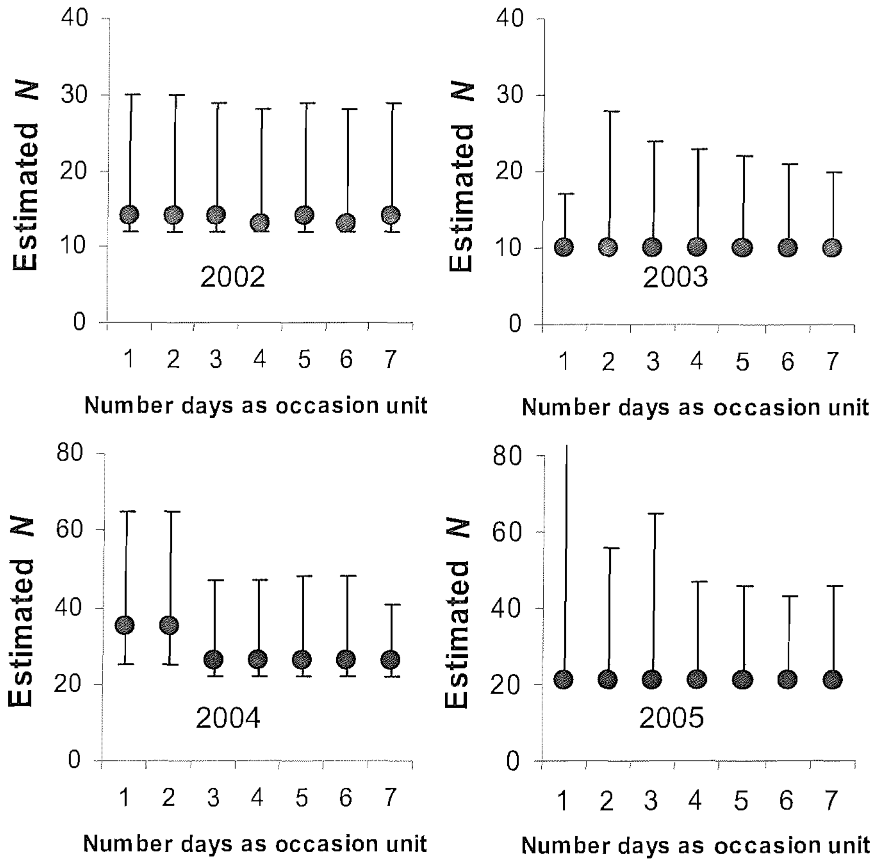

Figure 3.11 Abundance estimates for the four surveys. Seven abundance estimates are presented per study. Each of these seven uses a different unit of occasions for the estimate (1-day, 2-days, 3-days, 4-days, 5-days, 6-days and 7-days).

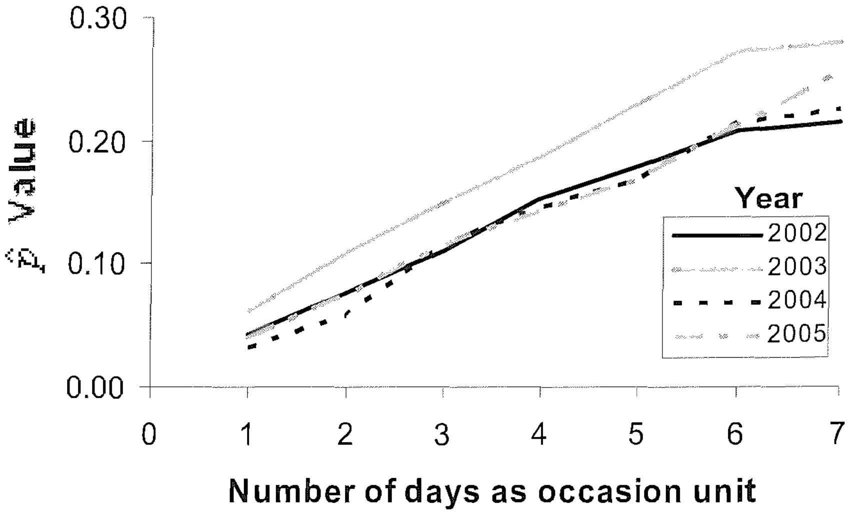

Figure 3.12. $\hat{p}$ values for the 4 years of data (each represented by a line) with increasing occasion unit length (from 1 day to 7 days).

### *Spatial variation in surveys*

Abundance and density of three separate areas within the main surveys were estimated to investigate the internal consistency of the surveys. Only those were analysed that had a full set of operational cameras for the entire survey. The null hypothesis of closure could not be rejected for the estimates of the "SSP" area and the "VIC" area, indicating they showed statistical closure. The hypothesis was rejected ($p < 0.05$) for all the "WEST" areas (including camera 20) and for "WEST(gate)" 2004 (excluding camera 20) meaning that statistical closure could not be assumed. The captures were not distributed evenly over the survey period for these surveys with more captures towards the end of the sampling period than at the start. This might indicate that new individuals were moving into the area towards the end of the survey period.

The density estimates were calculated for all the areas for comparison. The effective sampling areas were fairly similar in size for all three areas (SSP = 61.9 $km^2$, VIC = 62.4 $km^2$, WEST = 68.3 $km^2$, WEST(gate) = 55.7 $km^2$). Figure 3.13 shows that there was a high level of overlap between and within areas, especially for the SSP and VIC area. The WEST area showed more variation if camera 20 was included. The estimates for both 2005VIC and 2004WEST had low $\hat{p}$ values ($\hat{p}$ ~0.02) within the range of unreliability; 2004WEST had large confidence intervals while the estimates for 2005VIC seemed more acceptable. The relatively large difference between $\hat{p}$ value of 2005VIC ($\hat{p} = 0.0247$) and 2004WEST ($\hat{p} = 0.0163$) could explain the difference. The densities overlap with the complete survey density estimates presented in Figure 3.6. For both the SSP area and the VIC area there was a slight increase in mean density through time but there was consistency in density estimates between these areas per year.

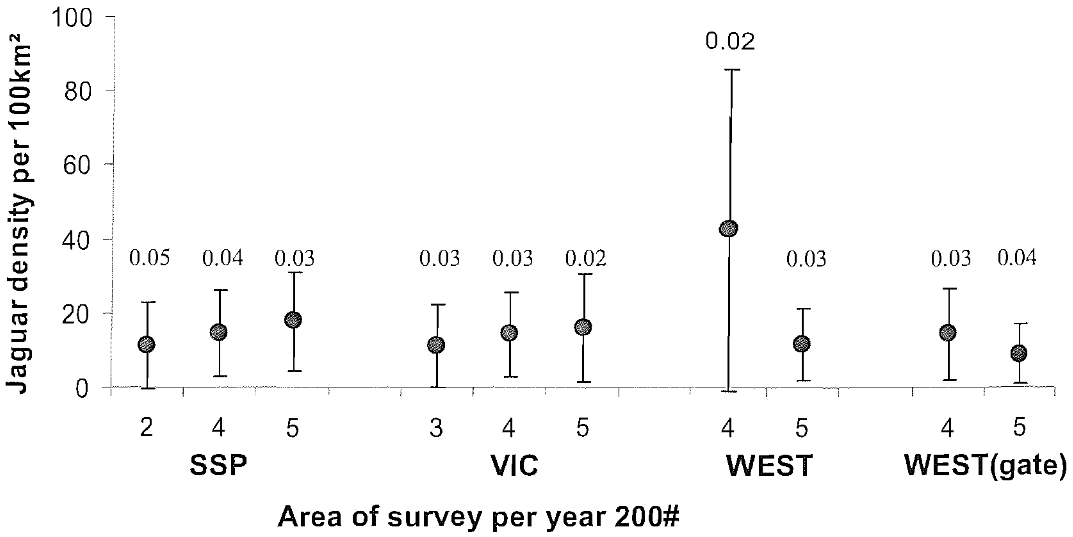

Figure 3.13. Density estimates for the three separate areas within the CBW survey. Sale Si Puede area (SSP), Victoria Peak area (VIC) and the Western trail area (WEST), with corresponding $\hat{p}$ values shown at the top of the estimate for each year. The results for the WEST area are also shown with the camera at the edge of the survey removed (WEST(gate)). Results are shown only for years that had a full set of cameras available for the entire period.

## Discussion

Camera trapping is the main method available for studying cryptic species living at low densities. Estimating abundance and density of such species can only be done with the use of mark-recapture analysis. The mark-recapture method was originally developed for large populations and its limitations have to be explored for applications to camera trapping of small populations. The generally low capture rate of cryptic species could limit the usability of the method for extremely low density populations. No published data are available on the limitations of mark-recapture analysis of camera trap data while its widespread use is foreseen for the near future. These limits were explored using simulation studies to manipulate the catchability of the populations.

The simulation studies showed that failure rates fell within acceptable limits (failure < 5%) as long as the catchability rate $\hat{p} > 0.03$, which is lower than the original recommendation of $\hat{p} > 0.1$ by White et al. (1982). Longer surveys (more occasions) allow a lower catch rate ( $\hat{p}$ ) still giving reliable estimates. The catchability has to be $\hat{p} \geq 0.05$ for the estimate to be both reliable and precise. The threshold of $\hat{p} \geq 0.05$ was confirmed by the relation between $\hat{p}$ and mean abundance for the data with sub-sampling with reduction of days. When $\hat{p} < 0.05$ mean abundance was overestimated. Conservation may fail if policy is based on an overestimated abundance of the target population. It is preferable for the management of a threatened or endangered species to be based on conservative (or even underestimated) population estimates.

Heterogeneity of $\hat{p}$ in the population could cause unreliability of estimates if a subset of the population has extremely low $\hat{p}$ values. The probability that an abundance estimate will be unreliable is increased the greater the difference between $\hat{p}$ values within the same population. High capture rates of certain individuals will decrease the reliability of the abundance estimate if other members of the population have low capture rates. As a general rule of thumb, a capture matrix should be explored for the level of heterogeneity and the number of individuals with single or low captures, before mark-recapture analysis commences. The overall $\hat{p}$ value of the CAPTURE output file should be $\hat{p} \geq 0.05$ for relatively precise results for a ~2 month survey.

Table 3.9 gives previously published data for large cat studies (jaguars and tigers). It shows that 9 out of 14 jaguar abundance estimates have a catchability of $\hat{p} < 0.05$ and 3 out of 14 have $\hat{p} \leq 0.03$ cut off point below which reliability is questionable. The tiger studies do much better in this respect, 7 out of 8 catchability values are higher than 0.1, except the study in Indonesia (O'Brien et al. 2003), which has a catchability $\hat{p} = 0.03$.

It is difficult to deduce the level of heterogeneity in catchability from the published studies but tables of jaguar recaptures indicated a substantial number of single captures. Levels of heterogeneity in $\hat{p}$ were high in the tiger studies of Kawanishi & Sunquist (2004) and O'Brien et al. (2003). O'Brien et al. (2003) only had 12 tiger captures of 9 individuals. This might give rise to potential problems of overestimation. No data were provided in this respect by Karanth & Nichols (1998).

It was assumed that the abundance estimates in the CBWS should be consistent over the 4 consecutive survey years since no environmental changes were observed in the region during this period. Indeed density estimates in, 2002 and 2003, were consistent as were the two separate density estimates sampled over 2 years in Tucavaca and Cerro Cortado areas of Bolivia (Table 3.9). In contrast, estimates from Gallon Jug in Northern Belize show inconsistency between years. The abundance and density estimates for the 4 surveys in CBWS were not consistent with a large jump in abundance between 2003 and 2004. The inconsistency could be explained by the overestimation of abundance in the year 2004 due to the low $\hat{p}$ value of 0.03. The inconsistencies across the years cause doubt on the overall reliability of the method in estimating density consistently.

The densities of the CBWS 2002 and 2003 fell within the range of densities for other jaguar studies while CBWS 2004 and 2005 were much higher (Table 3.9). The CBWS 2002 density estimate was similar to the Chiquibul density estimated in the same year on the other side of the mountain ridge from the CBWS. The Gallon Jug study is the only study that indicates similar density as the CBWS 2004 and 2005 but this survey also suffered from a low $\hat{p}$ value of 0.03 similar to CBWS 2004 which could indicate that the estimates were unreliable and probably overestimated.

Tiger and Jaguar densities as estimated by mark-recapture analysis of camera trapping data follow the expected pattern of density based on prey abundance in the study areas. Higher cat densities occur where there is higher prey abundance. The Gallon Jug area is well known for having a high jaguar population based on anecdotal evidence other than camera trapping. Herbivores reach high density with supplementary food from farmland crops and the owner of the land strictly enforces a no hunting policy. Estimates of jaguar densities in Bolivia are lower than estimates from Central America. The Cerro Cortado, Ravelo and Tucavaca areas are characterised as dry Chaco forest. The Madidi area is Amazonian rainforest at the foothills of the Andes. The Bolivian areas are characterised by a high diversity of prey species but low abundance of the individual prey species (pers comm. L. Maffei, research assistant Bolivia, Wildlife Conservation Society). The high density tiger parks in India (Kanha, Nagarahole and Kaziranga) are characterised by extremely high terrestrial herbivore populations and thus high tiger densities (Karanth & Nichols 1998). The tiger densities in the low density Malaysian and Indonesian jungles have low prey populations. The more arid Pench tiger reserve has medium prey densities (Karanth & Nichols 1998).

Any method to estimate abundance should be robust against minor changes in survey length or camera trap deployment as long as they fall within the limits of assumptions dictated by the method itself. The minor temporal and spatial variation between the survey years for the present study resulted in considerable differences between abundance estimates. When survey length and location was standardised between the years the annual abundance estimates were more similar than for the original survey data.

The influence of survey length on abundance estimates seemed to be mainly caused by a combination of low overall catchability and the ratio of presence : absence of captures. The erratic fluctuations in abundance estimates as survey length was reduced related to the changes in this ratio. Grouping of captures, by increasing the occasion unit length, increased the ratio of presence : absence of captures and this in turn increased the $\hat{p}$ value and precision of the estimates. Survey length is not of influence as long as $\hat{p}$ is high enough and does not show high variation between surveys. Abundance estimates derived from different periods of a long running survey were similar as long as the overall $\hat{p} \geq 0.05$, showing that such surveys are internally consistent and independent of the survey period. Robustness for changes in survey length can be assumed for $\hat{p} \geq 0.05$.

Eliminating sequential days from the capture data indicated that abundance estimates were not robust against changes in survey length if there was high capture heterogeneity; shortening a survey by just a few days led to overestimation of abundance in such surveys. All the published jaguar abundance estimates used single day occasions and had high levels of heterogeneity, giving rise to potential similar levels of overestimation. The tiger data do not have this problem because occasion unit was considered > 1 day, increasing the catchability and reducing heterogeneity. The catchability would have been much lower in these studies if a single day occasion unit was used for abundance estimates. Kawanish & Sunquist (2004) grouped 12 months of data into 9 occasions. O’Brien et al. (2003) grouped 6 months of data into an unspecified number of occasions. Despite the grouping abundance estimate was still left with the low $\hat{p} = 0.03$, casting serious doubt on the reliability. Although grouping of captures seems to be a suitable strategy for the two South East Asian studies, it creates another problem in terms of length of study. A survey length of 12 months or even 6 months is likely to violate the assumption of closed population for these studies (see Chapter 2). The Karanth & Nichols (1998) studies grouped the data in a different way by relocating cameras within a grid to different positions on a daily basis. This increased the spread of cameras reducing the chance of missing individuals due to poor camera locations (see below). The studies were carried out in the major tiger reserves of India with good road systems along which the cameras were deployed. Although allowing for better research, this situation is an exception since these parks are highly accessible and the tigers far less cryptic than generally in other tiger areas. The survey lengths did not exceed 3 months so should be within the limits of the closure assumption. Grouping of captures into longer occasion units should be considered when the overall $\hat{p} < 0.05$ for single day occasions. Increasing the occasion unit length will increase the overall $\hat{p}$ value, reduce heterogeneity and so increase the accuracy and precision of abundance estimates. Future studies of tigers in South East Asia should continue to group occasions but they should also attempt to increase the trapping effort to ensure that enough tiger individuals have a high enough capture rate in a 3-month period.

The study with the estimation of abundance after the removal of days from survey data indicated a positive linear relation between mean abundance estimate and $1/\hat{p}$. This relation should be further explored since the slope of this line could be an indication of reliability. Further study with a larger dataset from other areas is needed to draw adequate conclusions in this matter. The theoretical potential of the constant of the regression equation giving a reliable estimate for mean abundance should be studied further. Similarity between abundance measures and the constant could be another means of testing robustness of estimates.

Table 3.9 Density estimates for jaguars and tigers in different parts of the world. Data source: 1 = present study, 2 = Silver et al. (2004), 3 = Miller&Miller (2005), 4 = Miller (2005), 5 = Maffei et al. (2004), 6 = Karanth&Nichols (1998), 7 = O'Brien et al. (2003), 8 = Kawanishi&Sunquist (2004).

| Species | Name of area | Country of study | Density per 100km$^2$ | SE | $\hat{p}$ | Data Source |
|---|---|---|---|---|---|---|
| jaguar | CBWS 2002 | Belize | 7.2 | 2.28 | 0.04 | 1 |
| jaguar | CBWS 2003 | Belize | 5.8 | 1.46 | 0.06 | 1 |
| jaguar | CBWS 2004 | Belize | 18.5 | 5.98 | 0.03 | 1 |
| jaguar | CBWS 2005 | Belize | 11.1 | 5.55 | 0.04 | 1 |
| jaguar | Chiquibul | Belize | 7.5 | 2.74 | 0.07 | 2 |
| jaguar | Gallon Jug 2004 | Belize | 11.3 | 2.66 | 0.03 | 3 |
| jaguar | Gallon Jug 2005 | Belize | 8.8 | 2.27 | 0.05 | 4 |
| jaguar | Cerro Cortado I | Bolivia | 5.1 | 2.10 | 0.03 | 2 |
| jaguar | Cerro Cortado II | Bolivia | 5.4 | 1.79 | 0.05 | 5 |
| jaguar | Madidi | Bolivia | 2.8 | 1.78 | 0.04 | 2 |
| jaguar | Ravelo | Bolivia | 2.3 | 0.89 | 0.04 | 5 |
| jaguar | Tucavaca | Bolivia | 3.9 | 1.30 | 0.05 | 2 |
| jaguar | Tucavaca I | Bolivia | 2.6 | 0.77 | 0.04 | 5 |
| jaguar | Tucavaca II | Bolivia | 3.1 | 0.97 | 0.04 | 5 |
| tiger | Kanha | India | 11.7 | 1.93 | 0.18 | 6 |
| tiger | Kaziranga | India | 16.8 | 2.96 | 0.19 | 6 |
| tiger | Nagaraholo | India | 11.5 | 1.70 | 0.11 | 6 |
| tiger | Pench | India | 4.1 | 1.31 | 0.22 | 6 |
| tiger | Bukit Barisan Selatan | Indonesia | 1.6 | npd | 0.03 | 7 |
| tiger | Taman Negara site1 | Malaysia | 2.0 | 0.54 | 0.13 | 8 |
| tiger | Taman Negara site2 | Malaysia | 1.1 | 0.52 | 0.16 | 8 |
| tiger | Taman Negara site3 | Malaysia | 1.9 | 0.77 | 0.22 | 8 |

Choice of camera location seems to have a large influence on abundance estimates for the four CBWS surveys. Variation in camera location throughout the years was the main factor that influenced variation in abundance estimates. The changes in position of the cameras throughout the years improved the capture rate and capture of new individuals. The original camera locations may have caused some of the jaguars in this area to have a zero chance of capture, so violating the assumption for mark-recapture analysis (see Chapter 2). If a new camera location in the area increased the capture rate but still captured the same individuals in similar proportions as the old position then the abundance estimates would be similar between years. Presence of cameras is not enough to satisfy coverage of an area, the camera location must ensure that all the individuals in the area a catchability > 0. This can be achieved by locating one camera optimally or several cameras suboptimal but still cover the area for all individuals. It is difficult to judge the optimal location in advance. In this study it was judged in retrospect by comparing data between years and identifying increases in capture rate at new locations. Optimality of camera location cannot be judged for any of the other large cats studies since no information was given in the cited studies. The present data show that it is an important issue and should be taken into consideration. Karanth & Nichols (1998) probably had the least possibility of suffering ill effects from suboptimal camera location because cameras were rotated across several locations within a grid. They effectively used the strategy of more cameras covering the same position. This strategy is not possible for remote areas and careful considerations are required to strike a balance between covering larger areas and concentrating cameras with available resources.

The sub-sampling of the three independent areas within CBWS gave similar density results between years and areas (especially between areas in the same years). All areas had a high number of "high capture" cameras that could be considered in optimal locations. The similarity of the estimates for the three areas shows that there is consistency within the total study area if each area has a high number of optimal camera locations. This suggests that extrapolation may be valid to direct neighbouring none sampled areas with similar ecological and anthropogenic conditions.

Trapping effort seems to be the most important variable to successfully estimate abundance from a camera trap study. Further study is needed on the ideal distribution of cameras for capturing low density cryptic species. In Chapter 4 the influence of trapping effort will be further studied by using varying concentrations of cameras within an area. Further study is needed on optimal camera location and identification of habitat variables associated with high trap success. Camera trapping relies heavily on the funnelling a target animal past a camera. This will be different between different habitat types with varying levels of vegetation density. It is possible that the density differences observed in Table 3.9 are caused by differential success of camera trapping in different habitats. In Chapter 4 the habitat variables associated with capture rates will be further explored.

## Recommendations

Mark-recapture analysis of camera trap data to estimate of abundance of cryptic low density species is possible under certain conditions:

1) The overall catchability for a survey should be above a certain threshold: a minimum of $\hat{p} > 0.03$ for a 2-month survey with the full 60 occasions. The mean values will be more reliable for $\hat{p} \geq 0.05$. If $\hat{p} \leq 0.03$ then it is recommended to increase the occasion unit length by grouping occasions together.

2) The capture matrix should be studied prior to analysis to check for extremity in heterogeneity of capture. Although the Jackknife estimator allows heterogeneity but the simulation data show that high levels of heterogeneity cause unreliability. Grouping of occasions can reduce the level of heterogeneity.

3) A low overall catchability ($\hat{p} < 0.05$) raises susceptibility to erratic abundance estimates. The estimates should be calculated for different survey lengths by removing days from the capture matrix to create a similar abundance plot as Figure 3.8. The general distribution of means is more reliable than a single abundance estimate for the longest survey length.

It is recommended that a pilot study is performed before the real survey to test capture rates of potential locations. The emphasis of the pilot study should be on maximising variability of sites and final deployment should be based on maximum capture rate of a maximum number of individuals. The final trap configuration should be based on coverage of grids not on specific distances between cameras. This means that it might be necessary to put multiple cameras close together in an area when an area does not seem to have an optimal location.

# Chapter 4

# Effect on abundance estimates of camera trap distribution in space and time

## Abstract

Mark-recapture analysis using camera traps is the only method currently available to study large cryptic species living at low densities. Trapping effort and trap placement are the most important variables influencing the success or failure of mark-recapture studies for estimating population abundance. Little systematic research has been conducted on the effects of trap effort and design of trap placement to accurately and precisely estimate abundance using camera traps. This study investigates the trade-off between concentrating traps and distributing traps more widely for estimating abundance of jaguars in Belize. For a fixed number of camera traps, a wider distribution gave more reliable estimates provided optimal locations were used. Ideal locations for jaguars were mainly associated with wide, established trail systems independent of other habitat variables.

Any comparison of surveys between different times of the year in different areas requires that trap success, thus abundance estimates, is independent of season. Although variation existed no evidence was found abundance estimates or capture rates fluctuated with season.

## Introduction

The reliability of any method for estimating population abundance depends on sampling effort (Krebs 1994). For sign surveys, estimates depend on the number of sites visited, for distance sampling surveys the estimates depend on the length and number of transects and for a live trapping study the estimates depend on the number of traps, operational trap nights and the spatial distribution of the traps. Apart from sampling effort in terms of sample size it is important that the sampling sites (transects, grids or trap locations) are chosen so that they represent a given habitat type or optimize the chance of sighting or encountering signs of the target species. Seasonal changes in movement or fixed breeding seasons of target species can influence population estimates carried out at different times of the year. It is therefore important to understand such seasonal differences when carrying out a population estimate survey.

The three aims of this chapter are therefore: **1.** To study the effects of trapping effort on the precision and accuracy of mark-recapture studies. **2.** To study the ideal distribution pattern of traps for mark-recapture studies with a limited number of traps. **3.** To study ideal locations of traps and seasonal differences in abundance estimates and capture rate. The target species to study these aims will be jaguars in the Cockscomb Basin Wildlife Sanctuary (CBWS) in Belize using camera traps.

Relative abundance estimates based on trapping records of hunters or gamekeepers are often unreliable because trapping effort is variable and unknown. McDonald & Harris (1999) showed that the decreasing number of stoats (*Mustela erminea*) and weasels (*Mustela nivalis*) reported by gamekeepers over the years could be attributed to a lowered trapping effort and not necessarily a lowered abundance of stoats and weasels as was often reported. Ruette et al. (2003) found a similar variability in relative abundance based on trapping records for red foxes (*Vulpes vulpes*), stone martens (*Martes fiona*) and pine martens (*Martes martes*) in France.

The effect of trapping effort is most pronounced if the results of trap data are used as a raw index. In mark-recapture analyses trap effort will influence both the accuracy and the precision of the estimate. A minimum level of trap effort with an adequate distribution of traps is needed to ensure accurate and precise estimates. In mark-recapture studies trap effort depends on the number of trap sites and their distribution. Schlesser et al. (2002) compared estimates of small rodent abundance between small and large trapping grids in the same area. They found comparable results between the two but the precision suffered from the reduction in trap effort on the smaller grids. Density estimates seemed to suffer most because of increased edge effect (also see Chapter 2).

The current literature lacks investigations into effects of trapping effort on the precision and accuracy of mark-recapture abundance estimates using camera traps. The methodology has started to be used widely across the world but it is frequently employed to estimate abundance and density without questioning the reliability of the predictions (Karanth 1995, Karanth & Nichols 1998, O'Brien et al. 2003, Kawanishi & Sunquist 2004, Maffei et al. 2004, Silver et al. 2004, Maffei et al. 2005, Miller & Miller 2005, Miller 2005). The only study of the effect of camera trap effort on abundance estimates is Wegge et al's 2004 study of tigers in the Royal Bardia National Park in Nepal. They trapped intensively in a 25 km$^2$ area and sub-sampled the data by elimination of results to show that tiger abundance becomes underestimated with a reduction in camera trap density. An area of 25 $km^2$ is relatively small for studying tigers and it would have been useful to compare to less intensive data from a larger area. Such an analysis would have revealed the trade-off between camera density and survey area.

In this chapter the precision of camera trapping jaguars is studied by comparing abundance estimates of 'concentrated' surveys of high camera density over a small area with the estimates of the 'main' surveys, of lower camera density over a larger area. The numbers of captures and individuals were compared between sites of the main survey that overlapped the concentrated surveys to investigate the trade off of concentrating cameras in a smaller area or spreading them more widely. Density estimates were compared between the main surveys and concentrated surveys. Following Wegge et al. (2004), the concentrated survey data were sub-sampled to investigate the effect of a lower density of cameras on abundance estimates.

Ruette et al. (2003) showed that the success of hunting foxes, stone martens and pine martens with traps depended on the experience of the trapper and trapping method. Similarly, when using camera traps, it is important that the trap is placed in the optimal location for capturing the target species. Chapter 3 demonstrated that capture rate and number of individuals could alter dramatically when traps were re-located even short distances, and this had a measurable effect on the resultant abundance estimates. It is therefore important to identify which variables are associated with camera trap success, in order to give recommendations for future camera trap studies in dense jungle environment with low trap success. Maffei et al. (2004) studied the difference in capture rate of jaguars by comparing the results from camera traps on different types of trails in the Bolivian Chaco. They reported a high number of captures for jaguars on the larger size roads, medium number of captures on smaller trails and few near ponds and salt licks. No other habitat variables were studied. The camera traps for the concentrated surveys of this study were placed across a wide array of habitat types and trail sizes, including stream beds, different kinds of game trails and naturally open areas that could funnel the target species past the camera.

Variation in capture rate at different trap locations may reflect variation in habitat use by the target species. Little is known about the differential habitat use of jaguars and pumas. Scognamillo et al. (2003) radio-tracked several jaguars and pumas on the Venezuelan Llanos and did not find a significant difference in habitat use between the two species. Both species occupied similar habitat patches in similar proportions. Generally the jaguar is more often associated with lowland areas, rivers and streams whilst the puma is less associated with water and equally at home in high and low altitude areas (Emmons 1987). Frequency of capture associated with different habitat variables of a camera trap location was examined to investigate differences in use of habitat types.

None of the camera trap studies of large carnivores (Karanth 1995, Karanth & Nichols 1998, O'Brien et al. 2003, Kawanishi & Sunquist 2004, Silver et al. 2004, Maffei et al. 2005, Miller & Miller 2005, Miller 2005) indicated that the timing of the survey could have influenced abundance estimates yet seasonal variation in trap success is commonly reported in the literature, for example: foxes (*Vulpes vulpes*) in Britain (Baker et al. 2001), shrews and small rodents in tropical Africa (Nicolas et al. 2005, Stephenson 1994) and white-tailed deer (*Odocioleus virginianus*) in the United States (Naugle et al. 1995). The seasonal variation in trap success is often attributed to fluctuating availability of food and changes in the behavioural response to bait. Naugle et al. (1995) showed that the seasonal increase in juveniles caused the increase in abundance estimates for seasonal breeders like white-tailed deer. Seasonal breeding or seasonal differences in movement could influence abundance estimates based on camera trap surveys. It is important to understand the robustness of abundance estimates across seasons in different parts of the range of a species. Maffei et al. (2004) repeated camera trap surveys for jaguars in Bolivia during different seasons at two sites. The number of cameras and survey area were not similar between the seasons, making it difficult to compare capture rate or number of individuals captured. They nevertheless reported similar density estimates for both sites in the different seasons. Here we seek evidence of a seasonal trend in abundance estimates of jaguars or capture rate of jaguars and pumas. This was investigated by comparing the abundance estimate of a main survey conducted during the wet season of 2003 with the abundance estimates of the preceding and following dry season main surveys (2003 and 2004).

The objectives of this chapter are:

1) To recommend optimal deployment of a limited number of (camera) traps.
2) To evaluate the need to complement wide-scale surveys with concentrated surveys.
3) To assess the efficiency of camera traps as a tool for identifying habitat preferences and seasonality.

# Methods

Concentrated surveys, i.e. small scale surveys with high camera trap density, were conducted in five different areas within CBWS to evaluate the effect of camera density on: abundance estimates, number of individuals captured and total number of captures in comparison with main survey camera trap data in the same areas.

Table 4.1 shows logistical data for the 5 surveys in relation to main survey cameras. Data were discarded for failed stations thus the effective number of cameras used for analysis was "total stations" minus "failed stations". Figure 4.1 shows camera location and effective sampling area for the five concentrated surveys in relation to the main survey camera locations.

Table 4.1 Logistics of the five concentrated camera surveys. Main survey cameras "Same position" = number of cameras in the same location as main survey. "Within buffer area" = number of main survey cameras that fall within the buffer area (effective sampling area) of the concentrated survey.

| | | | | | **Main survey cameras** | | |
|---|---|---|---|---|---|---|---|
| **Name Survey area** | **Start survey** | **Survey days** | **Total stations** | **Failed stations** | **Same Position** | **Within Buffer Area** | **Buffer Area (km$^2$)** |
| 1 Western-Wari | 31-Jul-03 | 32 | 20 | 4 | 1 | 3 | 50.37 |
| 2 Antelope | 28-Dec-03 | 47 | 4 | 0 | 1 | 3 | 31.60 |
| 3 Juan Branch | 9-Jan-04 | 40 | 16 | 4 | 2 | 3 | 32.37 |
| 4 Mexican Branch | 1-Jun-04 | 45 | 22 | 2 | 2 | 5 | 45.07 |
| 5 access road | 20-Sep-04 | 43 | 16 | 0 | 2 | 5 | 70.62 |

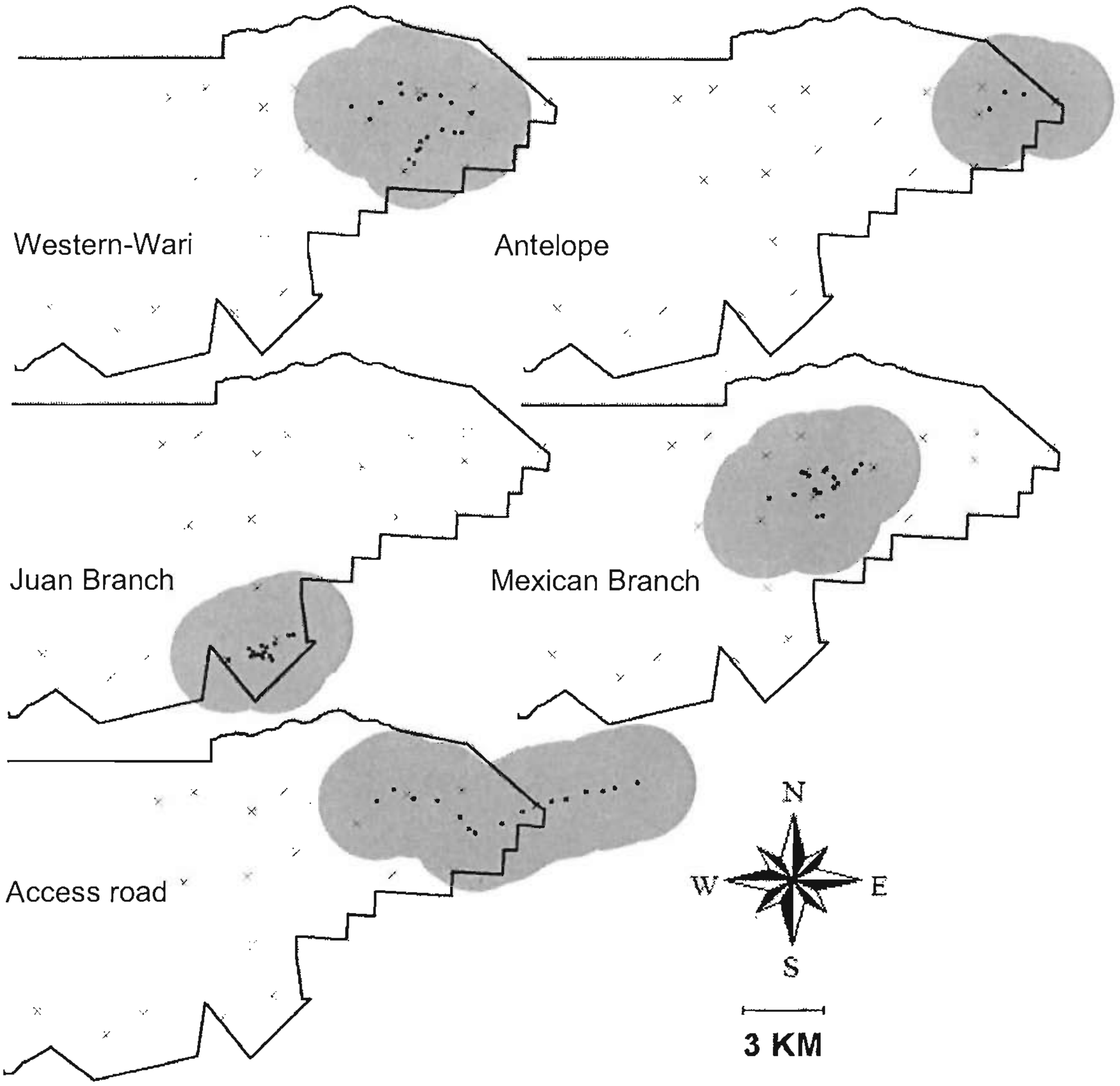

Figure 4.1 Camera locations and effective sampling areas for the five concentrated surveys. Black dots are camera locations, grey crosses are camera locations for the main survey. Grey area is the effective sampling area calculated with a radius of 2.36 km around each camera station (see Chapter 2).

## *Effects of camera density on abundance estimates*

### 1) Capture rate and number of individuals captured

The total number of jaguar captures and the number of individuals captured were compared between concentrated surveys and main survey cameras that fell within their effective sampling area. To evaluate whether a more dispersed camera deployment would capture more individuals than a concentrated deployment, the comparison was repeated with the inclusion of results of main survey cameras that fell outside of the effective sampling area of concentrated survey but whose buffer strip overlapped with the effective area of the concentrated survey (effective area with circle with 2.36 km radius around camera locations). Each of the concentrated surveys was compared with subsets of the main survey data. The main survey subsets were selected from periods closest in time to each concentrated survey with the same number of days as each concentrated survey.

All of the main survey cameras used for comparison were active for extended periods across multiple years. The number of captures were also calculated using the total capture rates of these cameras (captures/active days) and multiplying these with the number of days in the concentrated surveys.

### 2) Abundance and density estimates

Jaguar abundance was estimated for each concentrated survey using the program CAPTURE and density was calculated according to the method outlined in Chapter 2. These densities were compared to the density estimates from the four main surveys and the density estimates of the three separate areas of the main surveys: “SSP”, “Vic” and “West” (Chapter 3). Relations were explored between the mean densities, the standard errors and catchability estimates using Pearson correlations for the log10 transformed data. The relation between effective area and mean density was studied further for estimates with a catchability of $\hat{p} > 0.03$ ($\hat{p} < 0.03$ were deemed unreliable).

### 3) Abundance estimates with variable camera trap density

The data were sub-sampled by halving the density of the cameras in each of the concentrated surveys. Starting on one side of the survey area, alternate cameras were assigned to one of two separate survey groups (half1 and half2). The capture data for each group were used to create a matrix as an input for the program CAPTURE (see Chapter 2) which generated an abundance estimate for each group. For each concentrated survey the abundance estimate for each half was compared with the abundance estimate for the complete survey to reveal whether a reduction of camera density lowered the abundance estimates.

## *Habitat variables associated with jaguars and pumas*

For every camera location ($N = 119$) from all of the surveys (main surveys, concentrated surveys, line surveys, scrape surveys - see Chapters 7 and 9 for line surveys and scrape surveys), two measures of jaguar trap success were calculated for each camera: total captures, and total individuals, both presented as a percentage of all functional trap days. Functional trap days were defined as all the days a particular camera was effectively operational. Trap success of pumas was also calculated but only based on number of captures since it was not possible to individually recognise pumas (see Chapter 2).

Every camera location was scored on seven habitat variables (Table 4.2). Spearman rank correlation was used since some of the variables were rank scaled, to assess the strength of the relationships between the habitat variables and both jaguar and puma capture rates.

The continuous habitat variables (distance to river, distance to stream, width of trail, slope and altitude) were analysed in a stepwise regression, using Minitab version 14, to examine how much of the variance of jaguar and puma capture rate was explained by habitat. All variables were log10 transformed to approach a normal distribution. The default alpha level of 0.15 was used for entry and removal of variables. The camera traps along the access road, the widest trail in the analysis, were mostly avoided by pumas, therefore the analysis was repeated, excluding the access road data ($N = 110$).

Table 4.2 Habitat variables measured around camera traps. Width of trail is the mean width 20m before camera and 20m after camera. Age of trail:1 = old logging road kept open since establishment of the park in the 1990's, 2 = trail used for occasional warden patrols since 2000. 3 = trails cut for present study. Seasonal trail: 1 = open all year round, 2 = open for large part of the year and 3 = freshly cut for the present survey.

| Variable | Source (unit) |
|---|---|
| altitude | OS map (m) |
| slope | OS map (°) |
| distance to river | OS map (m) |
| distance to stream | OS map (m) |
| width of trail | measured in field (cm) |
| age of trail | local knowledge (scale 1,2,3) old → new |
| seasonal trail | local knowledge (scale 1,2,3) established → seasonal |

## *Effect of season on capture rate*

To investigate the effects of seasonality on abundance estimates and overall capture rate, the dry season main survey of 2003 was repeated in the wet season from 25th September until 30th November 2003 (67 days). In response to a high failure rate of cameras, data from many camera locations were discarded leaving 10 camera stations with continuous data for the entire period. Abundance estimates were compared for this wet season survey and for the four dry season main surveys, using only data from these cameras.

General Linear Models were used to investigate seasonal and year and to year variation in capture rate of jaguars and of pumas (Minitab version 14). The input variables (independent variables) were camera location as a random factor, year of study, period or month of study and the interactions between these variables. Capture rate (number of captures/100 days) of jaguar and puma was the dependent variable. No experimental design was done in advance to study the effects of camera location in relation to seasonal and yearly changes. For this reason several GLM models using subsets of the data were run to create a balanced design. Jaguar and puma capture rates were analysed for differences between dry season 2003 (February, March, April), wet season 2003 (September, October, November) and dry season 2004 (March, April, May) with the model:

Felid captures/100 days = Location | Period + $\varepsilon$

with 10 camera locations and 3 periods: (dry 2003, wet 2003 and dry season 2004).

A second GLM analysed differences between years for jaguar and puma capture rates with the model:

Felid captures/100 days = Location | Year | Month

with 16 camera locations, 3 years (2003, 2004 and 2005) and 2 months (March and April). Month was included in the analysis to study short term differences in capture rate. The 3-way interaction provided the error variance $\varepsilon$ against which all lower order effects were tested. The data were not log10 transformed since the residuals approximated to a normal distribution.

## Results

Table 4.3 shows that the number of individuals was not higher for the concentrated than the main survey cameras in the area and was lower for the comparison with main survey cameras with overlapping effective area. Although these differences were consistent for all five areas, they were not significant on a paired sample permutation test ($p > 0.05$) due to small sample size ($N = 5$). Thus the strategy of covering a larger area was preferable to concentrating cameras into a smaller area because it maximises the potential to capture additional individuals.

Only one individual, a female, was captured solely during a concentrated survey and not during a main survey (Juan Branch survey). The camera which caught her was in a main survey location. None of the off-trail cameras within the concentrated surveys captured any new individuals not captured in main surveys and the few individuals captured off-trail had relatively high capture rates within the main surveys.

The number of captures in concentrated surveys was generally higher than in the main survey cameras within the concentrated area since more cameras were available to make repeat captures of the same individuals occupying the small area. The estimated number of captures, based on the long term capture rates of main survey cameras, was consistently lower than the main survey period used for comparison, indicating a higher than average capture rate for these periods.

Table 4.3 Jaguar captures and the number of individual jaguars for: concentrated surveys, main survey cameras within the effective sampling area of the concentrated survey ("main survey") and the main survey cameras whose effective sampling area overlaps with the effective area of the concentrated survey ("overlap main survey"). "Capture" = number of captures during the period closest in time to the concentrated survey and "Capture est" = number of captures based on the long term capture rates for each camera location.

| Camera area | Unit of comparison | Western/Wari | Juan Br | Antelope | Mexican | Access |
|---|---|---|---|---|---|---|
| Concentrated survey | Capture | 18 | 18 | 17 | 6 | 47 |
| | Individual | 5 | 6 | 7 | 4 | 6 |
| Main survey | Capture est. | 5 | 8 | 13 | 8 | 15 |
| | Capture | 8 | 14 | 13 | 11 | 21 |
| | Individual | 4 | 5 | 6 | 4 | 6 |
| Overlap Main Survey | Capture est. | 13 | 13 | 15 | 14 | 18 |
| | Capture | 15 | 21 | 14 | 18 | 27 |
| | Individual | 6 | 7 | 6 | 5 | 7 |

## ***Density estimates from concentrated surveys***

Figure 4.2 shows large overall variation in estimated density between the 20 different surveys and sub-sampled surveys. The log10 s.e. of the density estimates was positively correlated with log10 mean density (Pearson correlation, $r = 0.87, p < 0.01, N = 20$) but negatively correlated with log10 catchability coefficient per survey ($r = -0.49, p < 0.05, N = 20$). Consequently density estimates from surveys with low catchability tended to have means that overestimate the true population size, as found in Chapter 3, and the true population density was most likely to reside in the lower part of the large s.e.

Two of the five concentrated surveys had low catchability ($\hat{p} < 0.03$) and consequently unreliable density estimates with large estimated s.e. ("conc Warie" and "conc Mex" surveys). The other three ("conc Ant", "conc Juan" and "conc Access") had high catchability coefficients with the "Access" survey having the highest catchability coefficient (0.16) and small estimated s.e. Both the "conc Ant" and the "conc Juan" survey had higher mean population estimates than the other surveys with reasonable $\hat{p}$ values. Only surveys with relatively large effective areas ( > 50 km$^2$) gave density estimates that were close together (Figure 4.3). Small effective sampling areas overestimated the density compared to surveys with larger sampling areas (Figure 4.3, < 50 km$^2$, for example the "conc Ant" and "conc Juan"). It can be concluded that the effective sampling areas of the "Antelope" and the "Juan Branch" surveys were too small to accurately estimate density even though the overall catchability was high.

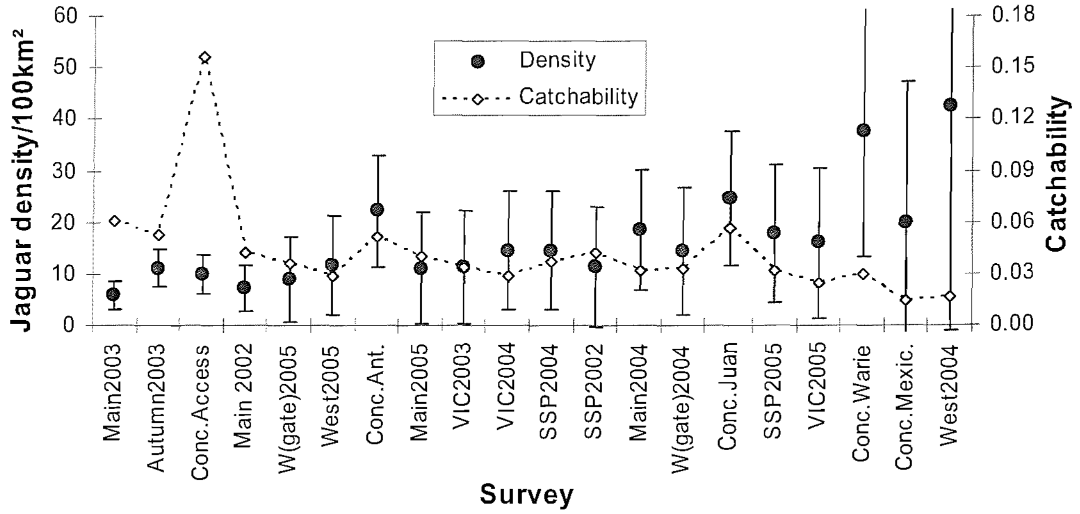

Figure 4.2 Jaguar density estimates and overall catchability for the 4 main surveys, 11 sub-sampled main surveys (Chapter 3) and the 5 concentrated surveys.The surveys are ordered by increasing density s.e. Standard errors lacking upper or lower markers fall outside of the range of the Y-axis.

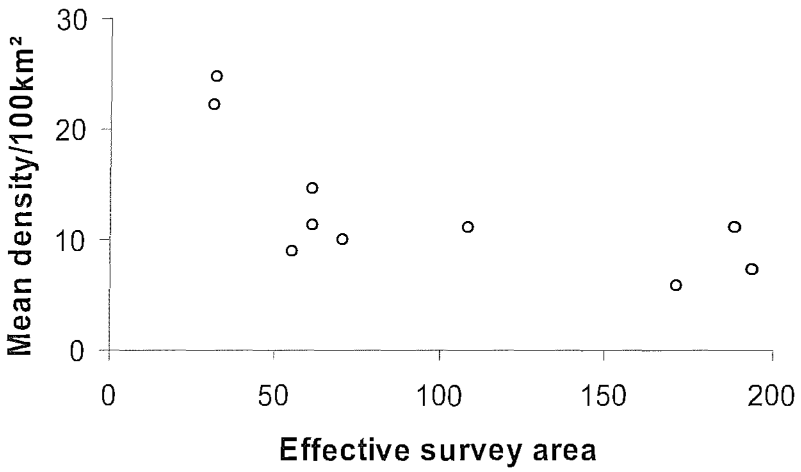

Figure 4.3 Scatter plot of all the mean density estimates displayed in Figure 4.2 with $\hat{p}$ > 0.03 and the effective sampling area.

## *Abundance estimates with varying density of cameras*

Figure 4.4 shows that there was a high level of overlap in abundance estimates between each concentrated survey (T) and it's two sub-samples (A and B). Reducing camera density had little influence on the abundance estimate within a survey area. Surveys with a reasonable catchability ($\hat{p}$ > 0.03) showed high overlap and internal consistency between the two sub-samples with half the camera density being adequate for abundance estimates. The reductions of camera density altered the catchability dramatically in the west-wari survey A (Figure 4.4). Individuals with only one or two captures were divided between the two survey halves with half A ending up with mainly individuals with higher capture rates.

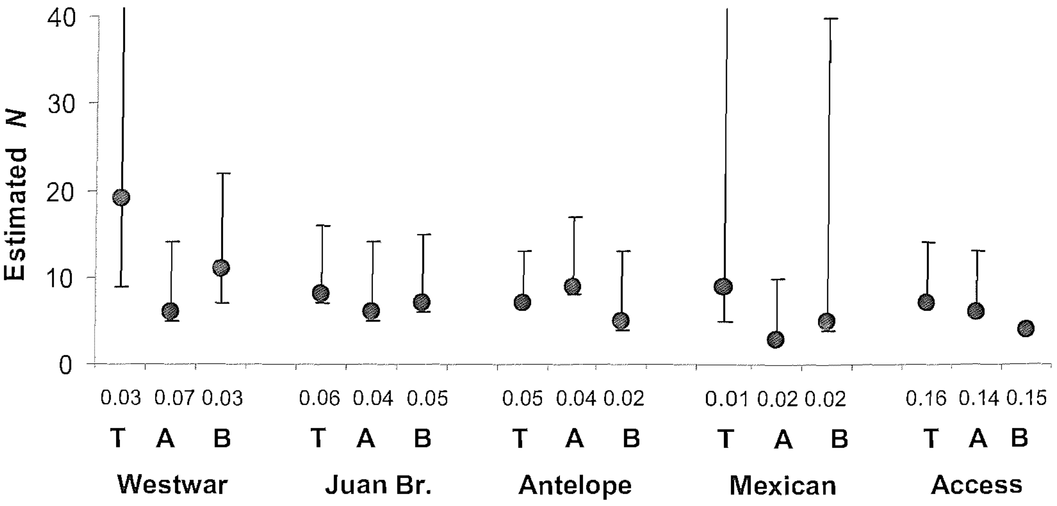

Figure 4.4 Comparison of the abundance estimates between each concentrated survey (T) and the two sub-samples (A and B). Standard errors range lacking upper or lower markers fall outside of the range of the *y*-axis. Catchability $\hat{p}$ for each survey is given at the bottom of the *x*-axis.

## *Habitat variables associated with jaguars and pumas*

The variables associated with trails had the highest correlation with capture rate for both cat species (Table 4.4). All trail variables were highly correlated with each other (width, age and seasonality). The older trails were also the wider trails and were not seasonal. Both cats preferred the wider established trails. The low positive correlation between captures and distance from rivers probably arose from a preference for larger trail systems over the smaller trails lying close to rivers rather than an avoidance of rivers per se. There were no significant correlations between capture rate and any of the other habitat variables and there were no differences between the cats. It can be concluded that jaguars and pumas frequent the habitat in the study area similarly.

Principle Component Analysis of the five continuous variables did not indicate a clear separation into distinct easy to explain dimensions but some relatedness could be observed between some of the habitat variables. Altitude and slope were related, with areas with higher altitudes generally having steeper slopes. Width of trail was negatively correlated with altitude since the larger old logging roads, which were the widest trails, were mainly located in the valleys. Width of trail was negatively correlated with distance to rivers since the old logging roads would avoid the swampier river bed areas.

Table 4.4 Spearman correlation matrix between habitat variables and jaguar and puma capture rate and individual rate per camera location. Correlations in bold are significant at $p < 0.05$. $N = 119$ camera locations.

| | Altitude | Slope | Dist.River | Dist.Str. | Width trail | Age trail | Seas.trail |
|---|---|---|---|---|---|---|---|
| **Altitude** | X | | | | | | |
| **Slope** | **0.54** | X | | | | | |
| **Dist. River** | 0.13 | 0.14 | X | | | | |
| **Dist. Stream** | 0.13 | -0.02 | **-0.24** | X | | | |
| **Width trail** | **-0.21** | 0.01 | **0.45** | -0.10 | X | | |
| **Age trail** | -0.14 | -0.17 | **-0.47** | -0.01 | **-0.66** | X | |
| **Seas. trail** | 0.11 | 0.10 | **-0.24** | -0.12 | **-0.53** | **0.80** | X |
| **Jaguar cap.** | -0.07 | -0.12 | **0.24** | 0.02 | **0.51** | **-0.59** | **-0.61** |
| **Jaguar ind.** | -0.08 | -0.10 | **0.22** | -0.06 | **0.42** | **-0.45** | **-0.46** |
| **Puma cap.** | 0.04 | -0.10 | **0.24** | 0.10 | **0.46** | **-0.55** | **-0.52** |

Stepwise regression identified trail width as the single most important explanatory variable of jaguar and puma captures (Table 4.5). Slope was consistently the second significant variable entered into the model, with lower slopes having higher number of captures, $p < 0.05$, but only explained a negligible part of the total $r^2$. Capture rate of both cat species increased with increased trail width. The Pearson correlation of the capture rate and trail width were higher for jaguars than for pumas ($r = 0.56$ with $p < 0.01$ for jaguars, $r = 0.36$ with $p < 0.01$ for pumas, for log10 transformed data). This difference was mainly caused by the contribution of the widest trail used in the study, CBWS access road. This road carries car traffic, 10-20 vehicles a day in peak season, and had many jaguar captures but few puma captures. Exclusion of the access road data from the analyses showed that puma capture rate had a stronger correlation with trail width than did jaguar capture rate ($r = 0.43$ $p < 0.01$ for jaguars, $r = 0.56$ with $p < 0.01$ for pumas, for log10 transformed data). A similar pattern was found for the stepwise regression (Table 4.5 lower panel). In effect, pumas were associated with larger trails deeper within the forest. This relation was less strong for jaguars in this region but jaguars were clearly comfortable walking along the wide access road which the pumas seemed to avoid.

Table 4.5 Stepwise regression with jaguar (left panel) and puma (right panel) capture rate as the dependent variable and the five continuous habitat variables as input variables. Upper panels = complete dataset of cameras, Lower panels = camera data excluding access road data. Alpha to enter or remove 0.15. *N* = 119 with 26 missing cases (upper panel). *N* = 110 with 26 missing cases (lower panel).

| **With access road** | **Jaguar** | | | **Puma** | |
|---|---|---|---|---|---|
| **Step** | **1** | **2** | **Step** | **1** | **2** |
| **Constant** | -1.42 | -1.29 | **Constant** | -0.71 | -0.59 |
| **Width trail** | 0.91 | 0.94 | **Width trail** | 0.59 | 0.61 |
| ***t*-value** | 6.55 | 6.94 | ***t*-value** | 3.74 | 3.94 |
| ***p*-value** | 0.00 | 0.00 | ***p*-value** | 0.00 | 0.00 |
| **Slope** | | -0.48 | **Slope** | | -0.42 |
| ***t*-value** | | -2.71 | ***t*-value** | | -2.04 |
| ***p*-value** | | 0.01 | ***p*-value** | | 0.04 |
| S | 0.38 | 0.37 | S | 0.43 | 0.43 |
| $r^2$ | 0.30 | 0.34 | $r^2$ | 0.12 | 0.15 |

| **Without access road** | **Jaguar** | | | **Puma** | |
|---|---|---|---|---|---|
| **Step** | **1** | **2** | **Step** | **1** | **2** |
| **Constant** | -1.30 | -1.06 | **Constant** | -1.99 | -1.79 |
| **Width trail** | 0.85 | 0.81 | **Width trail** | 1.23 | 1.20 |
| ***t*-value** | 4.43 | 4.29 | ***t*-value** | 6.34 | 6.21 |
| ***p*-value** | 0.00 | 0.00 | ***p*-value** | 0.00 | 0.00 |
| **Slope** | | -0.42 | **Slope** | | -0.37 |
| ***t*-value** | | -2.03 | ***t*-value** | | -1.75 |
| ***p*-value** | | 0.05 | ***p*-value** | | 0.08 |
| S | 0.38 | 0.38 | S | 0.39 | 0.38 |
| $r^2$ | 0.17 | 0.20 | $r^2$ | 0.31 | 0.32 |

## *Effect of season on capture rate*

There was a high level of overlap between abundance estimates of the three dry season surveys and the wet season survey (Figure 4.5). The mean abundance estimate of the wet season survey fell in between that of the 2003 dry season survey and the following 2004 dry season survey.

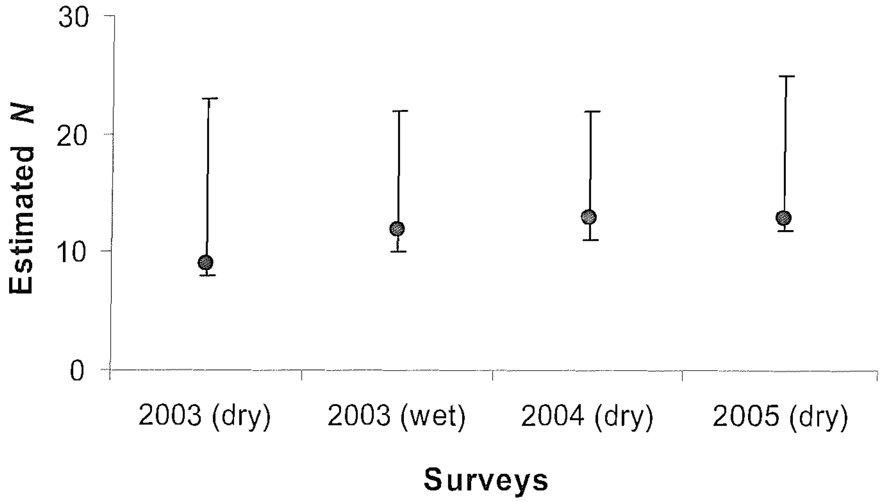

Figure 4.5 Abundance estimates of jaguars for three dry season (2003-2005) surveys and one wet season survey (2003).

Jaguar and puma capture rate did not differ significantly between the three periods (three periods: dry season 2003, wet season 2003 and dry season 2004; Table 4.6 and 4.7). The only differences that were found for both cats were differences in capture rate between camera locations.

Jaguar capture rates in March and April did not differ significantly between years or between the camera locations (Table 4.8). Puma capture rates differed significantly between camera locations between years ($p < 0.01$, Table 4.9). These patterns were found for the other combinations of the GLM models that were run including different months and years but not reported here. This meant that fluctuations in capture rates were generally only different between locations, not between seasons or years for both cats.

Table 4.6 GLM output: jaguar capture rates at 10 camera locations for three periods (dry season 2003, wet season 2003 and dry season 2004).

| **Jaguar** | **d.f.** | **SS** | **MS** | ***F*-value** | ***p*-value** |
|---|---|---|---|---|---|
| Period | 2 | 135.79 | 67.89 | 2.82 | 0.09 |
| Location | 9 | 590.84 | 65.65 | 2.73 | **0.03** |
| Period*Location | 18 | 433.18 | 24.07 | 1.20 | 0.29 |
| Error | 60 | 1200.17 | 20.00 | | |
| Total | 89 | 2359.99 | | | |

Table 4.7 GLM output: puma capture rates at 10 camera locations for three periods (dry season 2003, wet season 2003 and dry season 2004).

| **Puma** | **d.f.** | **SS** | **MS** | ***F*-value** | ***p*-value** |
|---|---|---|---|---|---|
| Period | 2 | 123.35 | 61.68 | 1.00 | 0.39 |
| Location | 9 | 3002.34 | 333.59 | 5.43 | **0.00** |
| Period*Location | 18 | 1106.68 | 61.48 | 1.35 | 0.19 |
| Error | 60 | 2724.04 | 45.40 | | |
| Total | 89 | 6956.42 | | | |

Table 4.8 GLM output: jaguar capture rates at 16 camera locations in March-April for the years 2003-2005.

| **Jaguar** | **d.f.** | **SS** | **MS** | ***F*-value** | ***p*-value** |
|---|---|---|---|---|---|
| Location | 15 | 1135.61 | 75.71 | 7.51 | 0.12 |
| Year | 2 | 28.67 | 14.34 | 0.68 | 0.51 |
| Month | 1 | 34.67 | 34.67 | 2.43 | 0.14 |
| Location*Month | 15 | 213.95 | 14.26 | 0.57 | 0.88 |
| Year*Month | 2 | 20.63 | 10.32 | 0.41 | 0.67 |
| Location*Year | 30 | 628.11 | 20.94 | 0.83 | 0.69 |
| Error | 30 | 753.39 | 25.11 | | |
| Total | 95 | 2851.03 | | | |

Table 4.9 GLM output: puma capture rates at 16 camera locations in March-April for the years 2003-2005.

| **Puma** | **d.f.** | **SS** | **MS** | ***F*-value** | ***p*-value** |
|---|---|---|---|---|---|
| Location | 15 | 1991.34 | 132.76 | 2.52 | **0.02** |
| Year | 2 | 146.56 | 73.28 | 1.67 | 0.21 |
| Month | 1 | 35.38 | 35.38 | 1.48 | 0.24 |
| Location*Month | 15 | 358.14 | 23.88 | 1.58 | 0.14 |
| Year*Month | 2 | 21.46 | 10.73 | 0.71 | 0.50 |
| Location*Year | 30 | 1315.21 | 43.84 | 2.90 | **0.00** |
| Error | 30 | 452.97 | 15.10 | | |
| Total | 95 | 4321.05 | | | |

## Discussion

It was shown in Chapter 3 that minor changes in camera location can influence abundance estimates of jaguars if moved from a low capture location to a high capture location. The influence of a low capture location is relatively minor if there is a high capture location close enough to sample the same area. It was recommended that a higher density of cameras should be used within an area as this would increase the chance that cameras were placed in high capture locations.

In this chapter, the concentrated surveys were used to test whether increasing density of cameras, by decreasing the survey area rather than increasing the number of cameras, influenced capture rate and abundance estimates. The number of captures and the number of individuals for the concentrated surveys did not warrant the higher density of cameras. Unlike Wegge et al. (2004) who found that tiger abundance in Nepal was underestimated as camera density was reduced, the abundance estimates in this study did not change when camera density of the concentrated surveys was halved.

The comparison between main and concentrated surveys suggests that the main survey trap density was adequate in which the maximum distance between cameras was based on a theoretical 10 $km^2$ circular home range (maximum distance between cameras is 3.5 km, see Chapter 2). In the trade-off between concentrating a fixed number of cameras in a small area or distributing the same number over a wider area, based on the minimum smallest home range of jaguars, the present data indicate that distributing the cameras over a wider area is the better strategy for increasing the number of individuals captured.

The effective sampling area of some of the concentrated surveys was probably too small (~50 $km^2$) for robust abundance or density estimates. The mean density estimates of the smaller concentrated surveys were higher than the mean density estimates for the equivalent main survey and the sub-sampled areas of the main surveys. It is likely that these were over-estimates were due to the effect of a high boundary to area ratio (see Chapter 2). Such an edge effect was described by Schlesser et al. (2002) in their comparison of density estimates of small rodents between small and large trapping grids. Distributing cameras more widely will reduce this edge effect. The main survey had similar density estimates to the four sub-sampled areas of the main survey (Vic, SSP, West and Access, mean size 80 $km^2$).

This suggests that quadrupling the sample area does little to alter the density estimate in this study. It cannot be assumed that that the area sampled by the main survey was large enough to reliably estimate the jaguar abundance and density. Rabinowitz & Nottingham (1986) found that the home ranges for five male jaguars ranged between 28-40 $km^2$ in the Cockscomb Basin. This translates to 5 or 6 exclusive home ranges within the effective sampling area of the main survey of ~190 $km^2$ (Chapter 3). If many individuals were captured at the edge of the area, with the majority of their range falling outside of the study area then the edge effect will likely cause an overestimation of the density. This could explain the high estimates in 2004 when 8 jaguars were captured only at camera 20 at the edge of the study area. Density estimates for conservation purposes need to be conservative and underestimation is preferable to over overestimation. Further investigation is underway into mean maximum distance moved by jaguars in Belize so as to better estimate minimum size of study area required (Yau, Silver, Harmsen, Foster in prep).

Almost all the captures in concentrated surveys were on main trails that were also represented in the main surveys. The off-trail camera locations of the concentrated surveys had low capture rates. The use of main trails for camera locations is preferable to off-trail locations because of the association with higher capture rate. Where established trails are present, cameras can be distributed at fairly low densities (~2 km between cameras). In areas of continuous forest, where no trails are present, it is hard to find suitable camera locations. The Mexican Branch survey, which did not have an extensive trail system, had the lowest jaguar capture rate. It is unlikely that this area has a lower jaguar density than the other areas comprising the main survey (Mexican Branch is prime lowland forest in the middle of the CBWS), rather it was more difficult to sample this area than the areas with established main trails. Similar low capture rates of tigers were observed in South East Asian tropical forest without trails (O'Brien et al. 2003, Kawanishi & Sunquist 2004).

Natural trails along stream beds had low jaguar and puma capture rates. Overgrown vegetation and steep banks can prevent animals using them as continuous corridors through the forest. In Africa and Asia, forest elephants create pathways which other animal utilise, but such mega-fauna are absent from the neotropics. The tapir (*Tapirus bairdii*) is the only species that could fulfil this role in the neotropics. However, they have relatively small home ranges and their association with water prevents them from creating extensive trail systems throughout the jungle. Many tapir trails begin and end in the middle of dense riparian vegetation where the tapir forages (pers. obs. B. J. Harmsen, thesis author).

Trail use by jaguars is well documented; even in the sparse dry shrub lands of the Chaco in Bolivia, jaguars were found to have preference for the larger roads and trails (Maffei et al. 2004). Both jaguars and pumas utilized the forest trail systems within the CBWS. Capture rate increased with trail width – the cats seemed to prefer to use the wider trails. Wide trails are more accessible and facilitate quiet, effortless movement through the otherwise dense forest. Of notable exception was the access road into the CBWS, the widest trail sampled in the study. Jaguars regularly travelled along the access road but puma capture rate was low and remains so to date (R. Foster pers comm. R Foster, PhD student, Southampton University). Vehicles pass into the CBWS on a daily basis, and the access road cameras lay closer to human habitation than did the other camera locations. Pumas may be more wary of humans than are jaguars. It is plausible that whilst jaguars navigate along or across highways, busy roads close to human development may deter the more cautious pumas, or even act as a physical barrier. Further study is underway within the neighbouring human-dominated habitat to explain these differences (Foster & Harmsen in prep).

Both jaguars and pumas used similar habitats. This corroborates the finding of Scognamillo et al. (2003) of similar habitat use by jaguars and pumas in the Venezuelan Llanos. Neither jaguars nor pumas were associated with water; nor did their capture rates vary with altitude or slope. The present study was conducted in the low-lying eastern area of the CBWS (maximum altitude of 240 m). It is likely that the variation of habitats sampled was not sufficient to detect a difference in capture rate with altitude and slope. Additional sampling is required in the rugged western area of the CBWS to better investigate the influence of altitude and slope on jaguar and puma capture rates. This is important for understanding jaguar connectivity throughout Meso- and Latin America. It has to be understood to what extent high altitudes and slopes form a barrier to jaguars since several mountain ranges exist within the jaguars range. Understanding the use of mountainous areas is also important for conservation. Lowlands are preferred areas of human development. If jaguars also prefer these areas then we need to prove rigorously the case of necessity for protection as high density jaguar areas.

There was no evidence for seasonal variation in the capture rates of jaguars or pumas. Behavioural changes can affect the local capture rate, for example when males begin to seek a receptive female, or when juveniles disperse from the natal home range. This study provided no evidence that such phenomena have a seasonal pattern which would otherwise increase or decrease the overall capture rate at certain times of the year. Similarly predators may change their behaviour in response to prey availability, for example to a seasonal calving season when there is a large influx of white-tailed deer juveniles (Naugle et al. 1995). The absence of seasonal variation in jaguar and puma capture rates implies that there is little variation in prey movement or availability. The knowledge that jaguar capture rate does not vary with season will allow population monitoring to be conducted at any time of the year; and allow comparison of density estimates from the same climatic region regardless of the season in which the data were collected. Seasonal differences in abundance estimates have to be studied further in areas with greater seasonality, for example: 1. wetland areas like the Pantanal in Brazil or the Llanos in Venezuela, where flooding of large areas causes contractions of jaguar home ranges in the rainy season to the few higher ground areas and expansion again in the dry season (Crawshaw & Quigley 1991; Scognamillo et al. 2003). 2. The dry areas of the seasonal Pacific forests of Jalisco, Mexico where jaguar home ranges contract around the few remaining water sources in the dry season and expand in the wet season (Núñez et al. 2002).

## Conclusions and recommendations

When the available number of cameras is limited, the choice of survey area and camera distribution is important to ensure reliable abundance estimates. This study investigated two strategies of camera deployment: The “dispersed” design distributes cameras over a wide area, with camera spacing based on a theoretical minimum jaguar home range of 10 km$^2$ such that maximum distance between neighbouring cameras is 3.5 km. This design maximised the number of individuals sampled as long as the camera locations were optimal. For both jaguars and pumas large established trails seem to have the highest capture rates and are presently the closest approximation to optimal camera locations. Study areas of > 80 km$^2$ seemed to give relatively consistent density estimates but it is recommended as a conservative estimate not to go below 150-200 km$^2$ for a camera grid.

The design of concentrated trapping is necessary in the absence of a trail system. In such a situation there are no obvious optimal camera locations so camera density must be increased at the loss of survey area to ensure adequate trap success. In areas of continuous forest it is therefore recommended that a trail system be established before a survey commences. Pilot studies will then need to be conducted to ensure that jaguars have begun to use the new trails. Consequently surveys in undisturbed, virgin forest, the areas which are least well known, will need considerable advance planning.

The strategy of relying on established trails for sampling a population could be the appropriate strategy for maximising the capture of individuals. There is still the possibility that certain members of a population with different social status, for example males or females, avoid locations with high capture rates. Chapter 5 will investigate variation in capture rates between the sexes and between individuals and in more detail to study whether trail use is biased within the population.

The habitat analysis showed that camera traps could be used for answering ecological questions about jaguars using capture rate as a means of preference for locations. The use of camera traps for answering ecological questions will be further explored in Chapter 5 by studying their ranging behaviour and social system in more detail.

# Chapter 5

# Ranging behaviour and demography of jaguars

# Abstract

In this chapter camera trap data are used to test hypotheses about demographic differences between jaguars in terms of spatial and temporal distribution patterns. Captures on cameras were strongly biased towards males, with more individual males being photographed and male individuals having a higher capture rate than females. Maximum distance between captures at different camera locations was larger for male than for female individuals. Spatial distribution of male jaguars was characterised by extensive range overlap with no stability in occupancy. Anecdotal evidence was found for territorial behaviour, specifically range changes in response to the disappearance of a single male. There was no evidence of avoidance behaviour between individual jaguars. This is the first time that camera trap data are used to answer questions other than abundance estimates and the methodology can be used as a template for future camera trap studies on cryptic species.

Open population models were used for the first time to estimate life history parameters of jaguars. This is the second study to use long-term camera trap data for open population models. The best fitting model showed 100% survival and 90% immigration into the area over 5 years.

# Introduction

Camera trap technology is used to estimate the abundance of cryptic species that are otherwise difficult to study, for example tigers (Karanth 1995, Karanth & Nichols 1998, O'Brien et al. 2003, Kawanishi & Sunquist 2004), jaguars (Silver et al. 2004, Maffei et al. 2004, Miller & Miller 2005, Miller 2005), leopards (Henschel & Ray 2003) and ocelots (Maffei et al. 2005). In principle, the data from this technology should be suitable for estimation of parameters other than abundance though this is rarely attempted. The aim of this chapter is to investigate whether and how camera trap data can be successfully used for estimating life history parameters and testing ecological hypotheses about the jaguar in the secondary broadleaf forest of the CBWS, Belize.

It is important to identify and understand demographic biases in individual catchability since this can influence abundance estimates based on camera trap data (Chapter 3). Individual catchability may vary with age, sex and social status, for example: juveniles walking with their mother are rarely captured on camera since they will pass the camera once it has triggered (pers. obs. B. J. Harmsen, thesis author); dominant individuals may deter subordinate individuals from areas of high conspecific traffic; shy individuals may avoid camera traps since these locations have been manipulated and are frequented by humans; males may utilise main trails more than females. Information about the social status of an individual cannot be extracted from single photographs and so it is not possible to investigate whether social variables influence the individual's catchability. Sex, however, can be deduced from photographs. In this study capture rates of males and female jaguars are compared to determine whether there is a sex bias in catchability.

A male biased sex ratio is common in camera trap studies. Four out of five camera trap studies in Belize and Bolivia, including the CBWS captured more male than female jaguars (Silver et al. 2004, Miller 2005). Published camera trap studies of tigers do not report sex ratios but also suffer a male bias (pers. comm. S. Silver, head of jaguar surveys, Wildlife Conservation Society). A male bias within trapping records is not only confined to feline camera trap captures. Hair captures for DNA studies exhibit a male bias for wombats (*Lasiorhinus kreffti*, Banks et al. 2003), American badgers (*Taxidea taxus* pers. comm. K. Larsen, Associated professor, Thomson Rivers University, Canada) and grizzly bears (*Ursus arctos*, Boulanger et al. 2004). Road kill surveys of red foxes in Japan found a male bias in the number of carcasses (Takeuchi 1994). It is important to identify the cause of the skewed sex ratio, whether it is a true bias or an artefact of the sampling procedure which can be rectified in future surveys. Three hypotheses could explain male sex bias in trap records.

Firstly, a real male bias may exist in the population. In this study this hypothesis was rejected because a polygamous population strongly biased towards males would probably be unstable and eventually crash. Le Galliard et al. (2005) showed experimentally that the increased competition for female lizards within a male-biased population reduced breeding and eventually led to extinction. The present evidence suggests a thriving population in the CBWS, sufficiently connected to other jaguar populations to ensure adequate gene flow and exchange. It is therefore unlikely that the CBWS jaguar population is strongly male-biased.

Secondly, sampling error may exist within the survey caused by the sexes favouring different areas such that males encounter a higher proportion of the traps. This hypothesis will be tested by comparing the capture rate of males and females at each camera location. Low capture rate of females relative to males at certain locations will indicate that the camera distribution used in this study was biased in favour of males.

Thirdly, sex differences in behaviour may result in different exposure rates such that the more mobile sex has an intrinsically higher chance of being captured. This hypothesis concerns behavioural attributes influencing capture frequency of males and females. If jaguars display the classic cat model in which the territory of one male overlaps with many females (see Chapter 1) one would expect a female bias (one male would have many recaptures on all the cameras and many females would each have a few recaptures, each female being photographed in a limited area). If males are less territorial, show a high level of overlap and cover larger distances, i.e. are more mobile, then a male bias would be expected because the effective sampling area is much larger for males than it is for females. This is investigated by exploring differences in capture rate, maximum distance moved and territorial behaviour.

Telemetry is frequently used to study the spatial distribution, social system territorial behaviour of big cat species (tigers: Sunquist 1981; leopards: Muckenhirn & Eisenberg 1973, Mizutani & Jewell 1998, pumas: Seidensticker et al. 1973, Hopkins et al. 1986, jaguars: Schaller & Crawshaw 1980, Rabinowitz & Nottingham 1986, Crawshaw & Quigley 1991, Núñez et al. 2002, Scognamillo et al. 2003, Lion (Hopcraft et al. 2005). This technique can provide continuous movement data on specific individuals, especially if GPS collars are used. Usually relatively few individuals can be studied at once and so the sample size from which to draw conclusions about the social system of the population is somewhat limited, while an unknown number of animals not collared could influence social behaviour in ways unknown to the researcher. In contrast camera traps can collect data on a large percentage of the population within an area, from a limited number of locations. Long-term camera data from fixed locations can be used to test hypotheses about the territorial behaviour of a cryptic species in terms of the spatial and temporal distribution of individuals at point locations.

Previous telemetry studies show that the spatial distribution of jaguars varies in different areas from almost mutually exclusive territories (Schaller & Crawshaw 1980, Scognamillo et al. 2002) to extensive range overlap between individuals (Núñez et al. 2002). Telemetry data from the CBWS showed that male jaguars have a high degree of overlap however the study did not include females (Rabinowitz & Nottingham 1986). There was evidence of territorial behaviour, territories shifted following the death of individual males and the neighbouring males extended their range to include parts of the range of the previous owner. In this study multiple years of camera trap data are used to describe ranges and range changes in the CBWS jaguar population over a 4 year period. Long-term camera data from fixed locations are used to assess the level of territoriality in males by describing the frequency distributions of: 1) number of individuals; 2) individual capture rates and 3) excess number of captures of the dominant individual over the next ranking individual; and also to describe the temporal stability of the dominance hierarchy in terms the rate of change and reversal of dominant individuals.

Jaguars are considered to be solitary (Emmons 1991). It is therefore predicted that males will actively pursue females and avoid or show indifference to other males. In this study long-term camera data from fixed locations are used to assess avoidance or attraction between individuals by: 1) comparing the time intervals between consecutive captures of same sex and different sex individuals and 2) comparing the distribution of consecutive captures of the same individual to a random distribution.

Mathematical models are useful tools for predicting changes in population size in the face of environmental change (Karanth & Stith 1999). Modelling populations requires a basic understanding of the relationships between life history parameters, recruitment, survival, emigration and immigration, of the target species and certain environmental and habitat parameters. Lack of such data is often the main constraint in predicting the fate of endangered species. Long-term camera data can be used to estimate life history parameters which would be otherwise impossible for cryptic species.

There are few estimates of survival, immigration and emigration of big cat populations due to the difficulty of acquiring reliable data and the lack of long-term studies that are necessary to acquire these parameters. Karanth et al. (in press) were the first to tackle this using long-term camera trap data. They used mark-recapture data collected over 10 years to estimate life history parameters of tigers. In similar manner to the Karanth et al. (in press) tiger study, here we use 5 years of annual survey data in a robust design open population model (Pollock et al. 1982) to estimate jaguar life history parameters. The robust design model will be used to estimate jaguar survival, recruitment, emigration and immigration for the first time.

The three objectives of this chapter are:

1) Investigate the causes of apparent male-biased sex ratio in camera trap data.
2) Seek evidence for territorial behaviour of the CBWS jaguars using long-term camera data from fixed locations.
3) Estimate life history parameters (survival, recruitment, emigration and immigration) of the CBWS jaguar population using open population analyses to model the data from multiple surveys carried out over 6 years.

## Methods

It is easier to assign an individual as a male than a female because the presence of testes is unmistakable (Figure 5.1). Individuals lacking testes were assigned as females. All jaguars with a reasonable trapping record were sexed. There were enough photographs with a clear view beneath the tail for each individual to confidently assign most individual a sex.

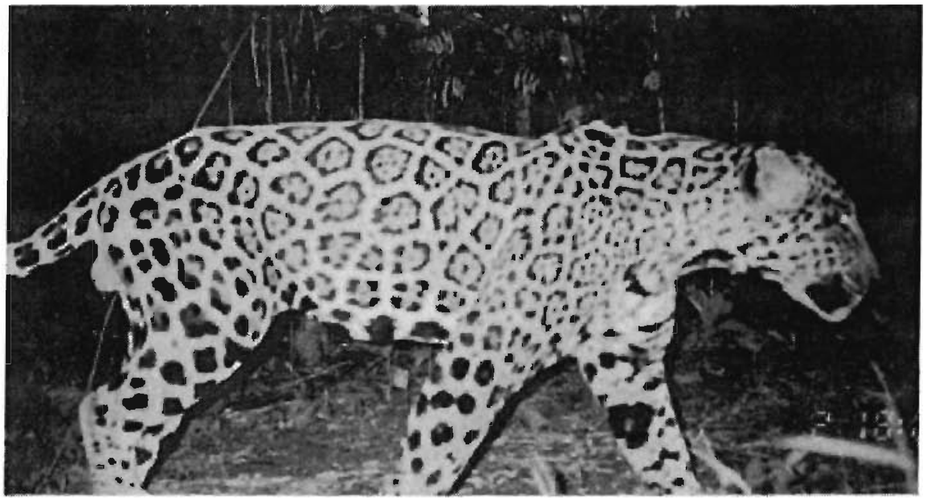

Figure 5.1 Male jaguar M00-1. The testes of the males are readily visible below the tail.

The total numbers of male and female individuals photographed during the study period (2002-2005) were used to calculate the overall sex ratio. An exact binominal test was used to test whether the sex ratio differed significantly from a 1:1 ratio. Consistency of the bias was tested for the twelve independent surveys completed throughout the 4 year period (see Chapters 3, 4, 7 and 9). The binominal exact test was used to test whether the 12 surveys showed a consistent significant pattern of bias toward one of the sexes.

## Causes of sex bias in camera trapping

Several hypotheses were tested, to examine whether the male sex bias was due to sampling error (the distribution of cameras was biased towards male captures) or behaviour differences between the sexes. To investigate sample bias between the sexes, capture rates of males and females were compared between all the different camera locations. A Pearson correlation was calculated between male and female capture rates at all camera trap locations (a significant negative correlation would indicate sample bias). Capture rates of males in locations where females were present were compared with capture rates of males in locations where females were not present (a significant difference with more males photographed in locations without females would indicate sample bias).

In order to test whether the male sex bias was caused by a behavioural attribute of one of the sexes two hypotheses were tested. First it was hypothesised that the maximum distance moved by males is greater than that the moved by females. The maximum distance between camera captures of individual males was compared with those of individual females. Individuals with less than 3 captures were excluded from the analysis. Second.it was hypothesised that males are more active than females. The total number of captures per individual for the whole study period was used as a measure of activity. Activity of males was compared with the activity of females.

All data were log10 transformed to approximate normal distribution and equal variance. Student *t*-tests, adjusting for unequal variance were used for all comparisons using Minitab version 14.

## *Territorial behaviour of jaguars*

Evidence for territoriality in the form of home range exclusivity was sought by investigating occupancy around camera locations throughout the study period. As a working hypothesis, it was expected that jaguars held exclusive territories. This meant that the frequency distribution of the number of individuals occupying a given camera location within any given month would peak at one individual. The number of individuals captured per month was calculated for each camera location for the total period that the camera was operational (from here on referred to as 'camera-month'). Only camera-months with multiple jaguar captures were used for the analysis. The level of territoriality was deduced from the frequency distribution. The more the distribution deviated from single individuals the less exclusive territoriality could be assumed for the population. Locations with long running cameras contributed more data than cameras running for shorter periods which meant that the data were not independent. To examine if this affected the results, the average number of individuals was calculated per camera-months per location. Biases were identified from comparison of the frequency distribution of both datasets.

The working hypothesis of dominance was that one individual would be dominant in an area. Individual capture frequencies per camera-month were used as an index of individual occupancy. Only camera-months with multiple individuals were included in this analysis. It was hypothesised that during any camera-month one individual would have a higher occupancy than the other individuals captured there, indicating their dominant status. Occupancy was only examined for males since the sample size for females was too low for analysis. Individuals' occupancies were ranked to produce a dominance hierarchy of occupation. The highest ranking individual (*D*) with most captures was assumed dominant at that camera location within the given month. The level of dominance for this individual was scored in terms of the excess number of captures it had over the next individual in the hierarchy (*ND*). The frequency distribution of excess captures (*D-ND*) revealed to what extent dominant individuals were present in the study area. The more the frequency distribution is skewed towards high values of *D-ND* per camera-month the more it could be assumed that dominance was prevalent in the study area. Some cameras had inherently lower captures than others, so less opportunity for excess captures. For this reason the frequency of excess scores was calculated per category of number of captures (e.g. cameras with 3 captures, cameras with 4 captures etc). For this analysis data were only included for > 2 individuals per camera-month. In similar manner as described above the data for this analysis could not be considered independent. To validate its use, the distribution of the average *D-ND* score per camera was compared with the complete distribution of *D-ND* scores.

The stability of occupancy at each camera location was examined using long-term trapping records (camera locations with > 3 months of trap data). Stability of occupancy was studied by calculating the number of changes in ID of the individual holding the highest "*D* score" through time. The number of changes in *D* at each camera location through time was divided by the number of months that the camera was functional. Ties in *D* per camera-month, two or more individuals with equal *D* scores, were scored as a change, unless one of the individuals in the tie had previously or subsequently held the highest *D*. The proportion of changes was calculated as the number of changes per camera location divided by the number of months that the camera was active. The mean of proportion of changes for all the camera locations was calculated as an index of overall stability of occupancy in the study area. This index ranged from 0 (no change in occupancy between months at all camera locations) to 1 (occupancy at every camera location changed every month). It was assumed that the higher the number of changes the less stable were the territories and the more the situation represents temporary occupation rather than territoriality.

A change in hierarchy does not negate territoriality since individuals can take over territories of weaker or dead individuals. A change does rule out territoriality if the previously ousted individual returns and becomes the dominant individual again. This special case of change was a reversal. A reversal was defined as a return to 1st rank by an individual who had temporarily gone down in rank. The number of reversals in *D* at each camera location through time was divided by the number of months that the camera was active. A similar index as for changes was calculated for the mean number of reversals (ranging from 0 to 1). A relatively high score in reversals indicated lack of territoriality in the jaguars in the study area.

## Attraction and avoidance

It was hypothesised that male jaguars would avoid other male jaguars but would be attracted to female jaguars. A time line of jaguar captures was created for each camera location to calculate the time intervals between captures of: the same male ("same male" captures), two different males ("male-male" captures) and of males and females (here "male-female" captures refers to captures of the two sexes in either order). All data were log10 transformed to approximate normal distribution and equal variance. Student *t*-tests, adjusting for unequal variance were used for all comparisons using Minitab version 14, except when stated otherwise.

## Attraction between males and females

The frequency distributions of time intervals between male-male captures and between male-female captures were compared using the hypothesis that the time interval between male and female captures was shorter than the time interval between captures of two different males.

The frequencies of the total male-female captures that fell on the same and different days were compared to the frequencies of the total male-male captures that fell on the same and different days, using a $\chi^2$-test for the hypothesis that male-female captures were more likely to occur on the same day than were male-male captures.

## Avoidance between males

The hypothesis was tested that the time intervals between captures of the same male individual were shorter than the time interval between captures of different male individuals.

A non-parametric runs test was used to test whether the distribution of captures through time of different males differed from a random distribution expected from negligible interaction between individuals. The level of clustering is inferred from the deviation of observed number of runs from the expected random distribution. A single run consists of consecutive captures of the same individual. A clustered distribution (few runs) occurs when individuals have more consecutive captures than expected at random, indicating avoidance between individuals. A regular distribution (many runs) occurs when individuals have less consecutive captures than expected at random, indicating attraction between individuals. Data were used only from camera locations with $\geq 3$ captures per individual and $\geq 2$ individuals. Individuals from each camera location were assigned an ID number according to capture frequency (the individual with the highest capture frequency = 1, 2nd highest = 2 etc). The data were then pooled by stacking the data from each camera location because the sample sizes were too low to perform the runs test separately for each camera location. This meant that several individuals could have the same rank. The runs test was performed on this pooled dataset to test whether the distribution of rank differed from random.

## *Individual ranging behaviour*

Maps were created to evaluate overlap in occupancy (based on capture frequency). Separate maps were created for males and females. Transient individuals, with only a few captures, were not included unless the individual subsequently was present with high number of captures. Only maps indicating patterns were shown, areas with many individuals and each having small numbers of captures were reported but not shown as a map. The length of the study period covered by each map was governed by timing between surveys or by shifts in individuals present (i.e. before and after a certain individual was present). The spatial distribution of occupancy and temporal changes were evaluated for evidence of exclusivity in home range use. The maps and descriptions are shown in Appendix B.

## *Open population mark-recapture models*

Jaguar population size, survival, emigration and immigration were estimated using open population analyses with robust designs within the program MARK (Cooch & White 2002). Robust design models are used for the estimation of life history parameters from short-term surveys which are repeated over longer time intervals, in this case ~2 months surveys repeated annually. The analysis is done in two stages: the first stage analysis performs closed population estimates for each short-term survey, in similar manner as done in Chapters 3 and 4, and these closed population outputs are used as an input for a second stage open population model to calculate the life history parameters of population abundance, survival, emigration and immigration, (Pollock 1982). Immigration and birth were combined as a single parameter, immigration, since these events cannot be distinguished from each other in the trapping record.

Five years of survey data (2002-2006) were available for these analyses. These comprised data from the 4 annual main surveys 2002-2005 (see Chapter 3) and data from an identical main survey conducted in 2006 (R. Foster & F. Yau unpubl. data). The matrices of capture data for each of the 5 annual surveys (see Chapter 2) were combined into a single matrix covering the entire period (2002-2006). The matrix consisted of a string of "zeros" and "ones" for each individual, with "one" indicating capture and "zeros" indicating non-capture (see Chapter 2). All individuals captured within the 5-year period were included; few individuals were captured every year therefore most individuals had years with zero captures within the matrix.

Apart from the four life history parameters, the open population analysis estimated two model parameters (capture rate and level of heterogeneity in capture rate). Heterogeneity of capture was modelled by allowing two capture rates (one high, one low) to be estimated each year.

The second stage yearly captures were collapsed into single capture records per year (present or absent) as an input for the program RELEASE (Burnham et al. 1987). The program RELEASE is based on Jolly-Seber models to calculate open population parameter estimates and includes a $\chi^2$ goodness of fit test of deviations from the two main assumptions of open population models: equal survival for all individuals in the population between years and equal capture rates for all individuals between years (Krebs 1994). The overall goodness of fit $\chi^2$was calculated by RELEASE (Burnham et al. 1987) and used as a measure of fitness of the data in similar fashion as for Karanth et al. (in press). The null hypothesis for the overall test is that survival and capture rates were equal between years. Rejection of the null hypothesis could indicate that the model was not fit for analysis by the robust design model.

Each of the six variables, four life history and two model variables, could be either homogeneous or heterogonous between years. Each heterogeneous variable had three, four or five parameters: five parameters for population abundance, capture rate and heterogeneous captures (one for each year), four for survival and emigration (the last year cannot be estimated) and three for immigration (the first and the last year cannot be estimated). Each homogenous variable had one parameter (constant for all years). Models of every combination were tested. The more parameterised the model, the better the fit to the data but the lower its explanatory power. Maximum likelihood theory and AIC values were used to resolve this trade-off by identifying the most parsimonious model as the one with the lowest AIC value (Cooch & White 2002). The model with the lowest AIC value was chosen as the most appropriate model. The weighted AIC value was used to indicate how much better the model was than the next best model. The higher the weighted AIC value above the other model, the better it is considered to be.

The use of open population models formally tested the assumption of Chapter 3 that the population was homogenous between the years, by identifying the population abundance parameter as either heterogeneous or homogeneous within the most parsimonious model(s). If heterogeneity was rejected, an overall population size could be compared with previous results of Chapter 3 from the program CAPTURE.

## Results

During the study period 2002-2005, 37 individual jaguars were photographed, five of unknown sex and of the remainder, a known ratio of 22 males : 10 females (binomial $p = 0.05$ of this arising from a 1 : 1 ratio in the population). The male bias was corroborated by the ratio of individual surveys, with 11 out of 12 surveys having more males than females (binomial $p < 0.01$ of this arising from a true ratio of half of all the sites having more males than females, Appendix D: Table D.1).

### *Sampling error in camera distribution*

Male capture rate was significantly higher in locations where females were present than in locations from which females were absent (means of 6.7 cap./100days and 3.9 cap./100days respectively, $t_{50} = 2.73, p < 0.05$, Appendix D: Table D.2). The number of male and female captures per location were significantly correlated (Pearson $r = 0.69, N = 71, p < 0.01$ following log10 transformation). This suggests that good camera locations for males were also good camera locations for females.

### *Behavioural differences between the sexes*

The maximum distance between captures of individuals was significantly longer for males than for females (means 8851 m and 4436 m respectively, $t_7 = 2.94$, $p < 0.05$, Appendix D: Table D.3). Males had higher activity than females (means of

14.4 and 3.9 captures per individual respectively, $t_{20} = 2.82$, $p < 0.01$, Appendix D: Table D.4). This showed that females travelled less far and were less active than males.

## *Territoriality of jaguars*

Camera-months with only a single capture were excluded, 115 for males and 31 for females. 123 camera-months had multiple captures, 108 for males and 15 for females. Figure 5.2 shows that most frequently two males were photographed at the same camera location within the same month. This pattern differs distinctly from the expected pattern of exclusive territories which would peak in the frequency of single individuals. Instead the observed pattern indicates a high level of overlap between males. This pattern was not apparent for females, although their sample size was small. Most frequently only one female passed a given camera within a month. The independent dataset, with mean number of individuals/month per single camera, inset of Figure 5.2, showed a similar pattern to the main figure, indicating that male jaguars did not have exclusive territories.

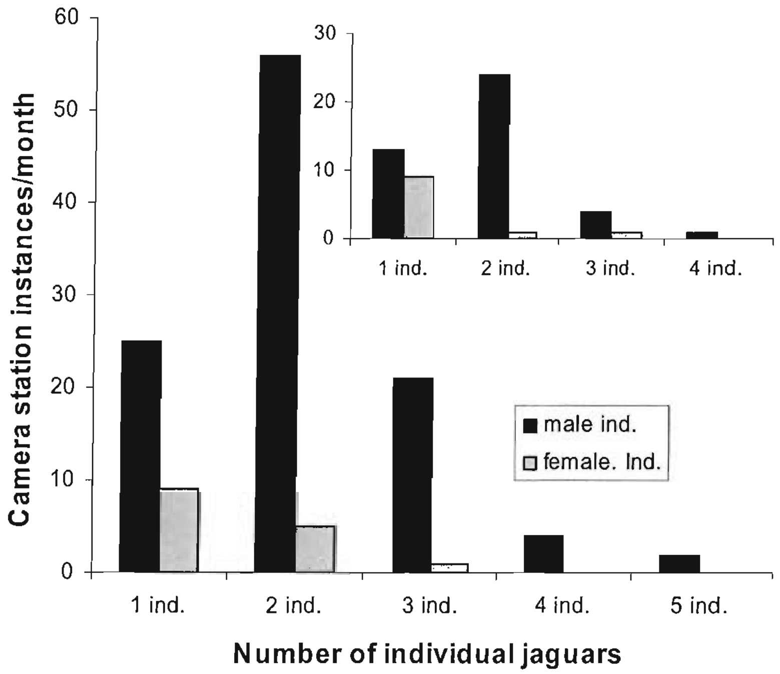

Figure 5.2 Number of individual jaguars photographed per camera per month. Only camera-months with more than one capture of either sex were considered (*N* males = 108, *N* females = 15). The inset shows the same frequency data as the main figure but using the mean number of individuals per month per camera (*N* males = 42, *N* females = 11).

Figure 5.3 shows the frequency distributions of excess captures of the dominant individual over the next dominant individual for camera-months with three captures ($N = 26$), four captures ($N = 13$) and ≥ five captures ($N = 19$, range 5-12, with $N = 7$ for 5 captures as the highest). 32 camera-months only had two captures which by definition had a zero *D-ND*, two individuals with one capture each (shown in Figure 5.3 as the bar with diagonal lines). The data showed that, independent of the number of captures, an excess score of one had the highest frequency. Low frequencies of capture-months had excess scores > one. The dataset in the inset of Figure 5.3 shows a similar pattern as the main figure. The pattern did not conform to a dominance distribution of territoriality for which it was expected that one individual would have a much higher frequency than the other individuals captured in the same camera-month giving a skewed distribution with a higher mean. Instead it seems that individual male jaguars were not dominating camera locations.

There was little evidence of consistent occupation through time. The mean proportion of reversal and change in the dominance was relatively high for all camera locations (Table 5.1). On average, 20% of the cameras show reversals in dominance ranking between months and 50% of the cameras show a change in dominance ranking between months. Few of the camera locations had no change or reversal in dominance. Two long-term camera locations ( > 7 months) which had a high capture rate had no reversals indicating consistency in occupancy. Of these two cameras only one had no changes meaning that some level of long term occupancy (territoriality) could be assumed for this location.

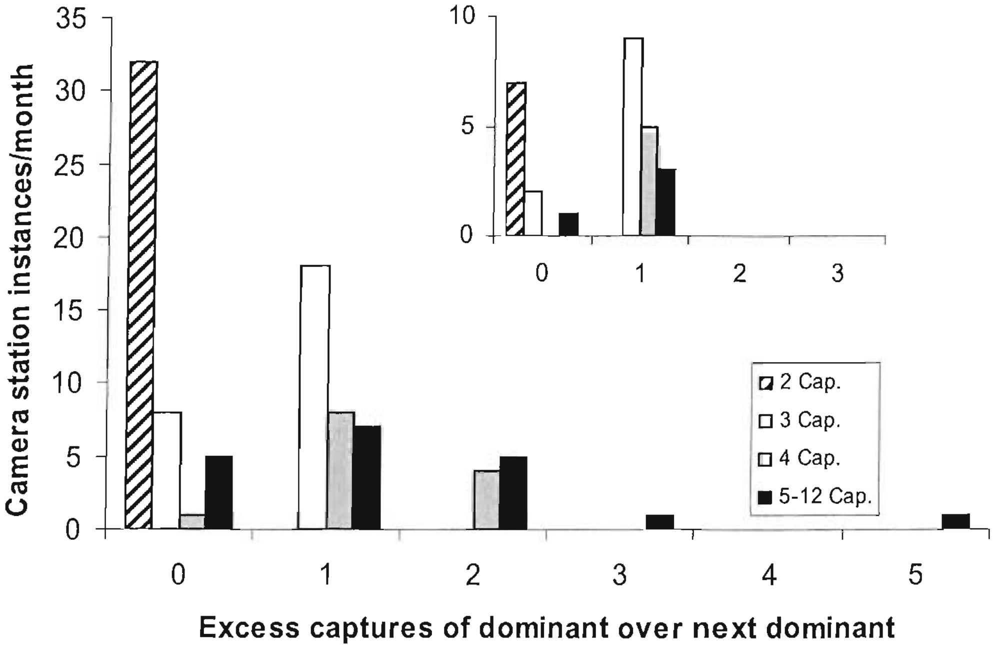

Figure 5.3 The percentage of monthly instances for excess number of captures for the dominant jaguar $N = 108$. Four different categories were used for distributions based on the number of captures per camera month: 2 captures, 3 captures, 4 captures and ≥5 captures. The inset shows the same frequency data as the main figure but for the mean number of excess scores per month per camera ($N = 36$).

Table 5.1 The mean proportion of reversals and changes per camera in dominance hierarchy of individual male jaguars per month. Change = different individual occupying the top rank. Reversal = an individual who previously occupied the top rank regaining the top rank position. *N* (tot) is the total number of camera locations used. *N* (0) is the number of cameras that have no reversals or changes.

| | | Proportion per Camera | | | Zero Changes | | |
|---|---|---|---|---|---|---|---|
| | ***N* (tot)** | **Mean** | **St. Dev.** | ***N* (0)** | **long term camera** | **short term camera** | **few captures** |
| **reversals** | 21 | 0.20 | 0.17 | 7 | 2 | 2 | 3 |
| **changes** | 21 | 0.50 | 0.23 | 2 | 1 | 1 | 0 |

## *Attraction and avoidance between males and females*

The sample size of male-male captures (248 events) was higher than for male-female (or female-male) captures (67 events). Only 7% of male-male captures were on the same day, compared to 14% of male-female captures (Figure 5.4; $X^2 = 4.2$, d.f.

= 1, $p < 0.05$, Appendix D: Table D.5). The time interval between captures was most frequently 1-5 days for both male-male and male-female captures (Figure 5.4). The frequency of capture pairs decreased as the interval length increases above 5 days. The time interval between male-female captures was not significantly different from the time interval between male-male captures (mean 6.5 days and 7.5 days respectively, $t_{93} = -0.96, p = 0.34$, Appendix D: Table D.6). These results indicated that overall attraction between male and females was weak and only present in the short-term.

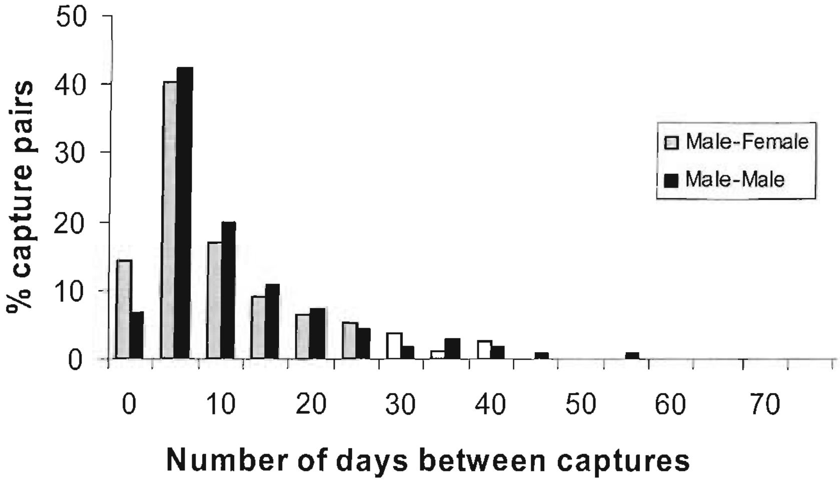

Figure 5.4 The number of days between captures of different individuals.
*N* male-male captures = 248. *N* male-female captures = 67

## Avoidance of males

The sample size of male-male captures (251 events) was higher than for same male captures (151 events). There was no evidence that different males avoided one another. The time interval between consecutive captures of different males was significantly shorter (by ~1.5days) than the interval between consecutive captures of the same male (mean 7.2 days and 8.6 days respectively, $t_{318} = -1.63, p < 0.05$, Appendix D: Table D.7).

Data on 463 captures of 22 males across 26 camera locations were used to test the level of clustering in captures of different individuals. There was no evidence of avoidance or attraction. The distribution of captures for the different males was not different from random, meaning that there was no evidence of mutual avoidance or attraction (the distribution was neither clustered nor regular: 219 runs of consecutive male-male captures observed, 232 expected, average $K = 0.48$, $p = 0.23$, Appendix D: Table D.8).

## Open population models

The null hypothesis of equal survival rates and equal capture rates between years could not be rejected using the collapsed data for the program RELEASE, therefore the robust model could be applied to the data (Goodness of Fit test $X^2 = 7.11$, d.f. = 5, $p = 0.21$). Table 5.2 shows the top ten best-fitting models based on the lowest AICc values. The difference between the models below this point was negligible (AICc weights < 0.01).

The parameter for population size ($N$) was constant for all 10 models, heterogeneity ($pi$) and capture rate ( $\hat{p}$ ) were constant for the models with the eight lowest AICc values. Thus, the models which best fitted the data (least deviated from the fully parameterised model) had constant population size, equal capture rates and equal levels of heterogeneity in capture rate; and any variance between years was explained in terms of emigration, immigration and/or survival. The AICc weights for the first three models were similar and higher than the remaining models. The estimated parameter values were therefore based on these three models, described in Table 5.3 for Model 1 and Model 3. The life history parameters of Model 1 were all heterogeneous while the life history parameters of Model 3 were all constant between the years. The parameter estimates of Model 2 were similar to those of both models in Table 5.3.

Table 5.2 The ten best fitting parameterised open population models for the surveys from 2002 until 2006, based on AICc. X = parameters that are constant across all 5 years, blanks = parameters that vary between the years. *Imm* = Immigration, *Emi* = emigration, *S* = survival, *pi* = capture heterogeneity, $\hat{p}$ = capture rate, *N* = population size.

| | Variables in model | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| Model | *S* | *Emi* | *Imm* | *pi* | $\hat{p}$ | *N* | AICc | Delta AICc | AICc Weights | Num. Par |
| 1 | | | | X | X | X | 705.11 | 0.00 | 0.29 | 9 |
| 2 | X | X | | X | X | X | 705.28 | 0.16 | 0.27 | 7 |
| 3 | X | X | X | X | X | X | 705.92 | 0.81 | 0.19 | 6 |
| 4 | | | X | X | X | X | 707.48 | 2.37 | 0.09 | 9 |
| 5 | | X | X | X | X | X | 709.40 | 4.28 | 0.03 | 9 |
| 6 | | X | | X | X | X | 710.31 | 5.19 | 0.02 | 10 |
| 7 | X | | X | X | X | X | 710.36 | 5.25 | 0.02 | 9 |
| 8 | X | | | X | X | X | 710.91 | 5.79 | 0.02 | 10 |
| 9 | X | X | | X | | X | 711.13 | 6.02 | 0.01 | 11 |
| 10 | | | | | X | X | 711.20 | 6.08 | 0.01 | 13 |

When all life history parameters were held constant (Model 3) survival was estimated as 100% (s.e. = 0.1). This estimate was probably inflated by the recapture of an individual in 2006 which had been absent since 2002; any other disappearances from the record were consequently explained by emigration rather than mortality. Emigration was estimated as 33% (s.e. = 7), immigration was estimated as 91% (s.e. = 8) and the population size was estimated as 12.49 (s.e. = 1.03). The standard errors for these estimates were relatively low.

When survival, immigration and emigration were set as heterogeneous (Model 1) they all showed considerable year to year variation. Survival followed the captures of individuals between the years. Survival of individuals captured in 2002 was estimated at 100% (s.e. = 0.001). This decreased to 75% (s.e. = 14) in 2003 and further to 57% (s.e. = 11) in 2004 as there was a high influx of individuals in 2004 that were never recaptured. In 2005 survival increased to 100% (0.001%) as most of the individuals were recaptured in 2006. Emigration in 2002 was 28% (s.e. = 17) and 33% in 2005. There was no emigration in 2003 as all individuals captured in this year were also captured in subsequent years. There was no emigration in 2004 as all individuals captured in this year were either captured the next year or never captured again. Immigration was 52% (s.e. = 39) between 2002 and 2003. Between 2003 and 2004 immigration was 100% (s.e. = 0.001); the population effectively doubled due to an extreme influx of individuals. In 2005 no new individuals were captured that had not been captured in previous years therefore immigration was 0% (s.e. = 0.001).

Estimates of immigration exceeded the estimates of emigration over the 5-year study period causing a temporary increase in the population estimates over time.

Both models estimate two capture rates $\hat{p}$ (captures/week) for the population, a high capture rate (0.54 cap./week) and a low capture rate (0.17 cap./week). This indicates that a sub-group of the population had a capture rate that was approximately one third that of the rest of the population. All ten models were chosen with the population size *N* constant between the years meaning that that the assumption of constant population size in Chapter 3 was true.

Table 5.3 Parameter estimates based Model 1 and Model 3 (Table 5.10). *S* = survival (range 0-1), *Emi* = emigration level (range 0-1), *Imm* = immigration level (range 0-1), *pi* = capture heterogeneity (range 0-1), *p* = capture rate (captures/week), *N* = population size.

| **Model 1** | **Estimate (s.e.)** | **C.I. range** |
|---|---|---|
| *S* 2002 | 1.00 (0.00) | 1.00 - 1.00 |
| *S* 2003 | 0.75 (0.14) | 0.41 - 0.93 |
| *S* 2004 | 0.57 (0.11) | 0.35 - 0.77 |
| *S* 2005 | 1.00 (0.00) | 1.00 - 1.00 |
| *Emi* 2002 | 0.28 (0.17) | 0.07 - 0.66 |
| *Emi* 2003 | 0.00 (0.00) | 0.00 - 0.00 |
| *Emi* 2004 | 0.00 (0.00) | 0.00 - 0.00 |
| *Emi* 2005 | 0.33 (0.13) | 0.14 - 0.61 |
| *Imm* 2003 | 0.52 (0.39) | 0.05 - 0.96 |
| *Imm* 2004 | 1.00 (0.00) | 1.00 - 1.00 |
| *Imm* 2005 | 0.00 (0.00) | 0.00 - 0.00 |
| *pi* | 0.37 (0.08) | 0.23 - 0.53 |
| $\hat{p}(1)$ | 0.54 (0.05) | 0.45 - 0.62 |
| $\hat{p}(2)$ | 0.17 (0.03) | 0.11 - 0.24 |
| *N* | 12.31 (0.96) | 11.36 -15.73 |

| **Model 3** | **Estimate (s.e.)** | **C.I. range** |
|---|---|---|
| *S* | 1.00 (0.00) | 1.00 - 1.00 |
| *Emi* | 0.33 (0.07) | 0.21 - 0.48 |
| *Imm* | 0.91 (0.08) | 0.60 - 0.98 |
| *pi* | 0.37 (0.08) | 0.23 - 0.53 |
| $\hat{p}(1)$ | 0.53 (0.04) | 0.45 - 0.62 |
| $\hat{p}(2)$ | 0.16 (0.03) | 0.11 - 0.23 |
| *N* | 12.49 (1.03) | 11.44 -16.08 |

# Discussion

The apparent male bias of jaguars in the CBWS camera trap records is unlikely to reflect the true situation when combined with information on capture locations, it can be explained more logically in terms of the difference in ranging behaviour between the sexes. Males were shown to be more mobile than females, they travelled further, were more active and did not have exclusive home ranges. Consequently, within a fixed survey, the effective sampling area of males was much larger than of females. Males had a higher probability of capture because they are likely to encounter more cameras, more frequently.

The capture rate of males within this study was 3-4 times as high as the capture rate of females. A high level of heterogeneity in capture rate within a population can result in unreliable abundance estimates when using closed population models (Chapter 3). Since the difference in capture rate is probably a consequence of sexual differences in jaguar behaviour rather than sampling error in camera location, this problem cannot be easily resolved by altering the survey method. Rather it is suggested that the abundance estimates be calculated just for the subset of the population with high capture rate, i.e. the males, and subsequently extrapolated to the female population with the assumption of an equal sex ratio. This requires more research at sites with less skew in the sex ratio since the problem of extrapolation becomes one of understanding the difference in effective sample area for the two sexes.

The difference in ranging behaviour of the two sexes will also influence density estimates. The effective sampling area used to estimate jaguar density in CBWS was based on half the mean maximum distance moved (MMDM) by individuals in the study (after Wilson & Anderson 1985, see Chapter 3 and 4). Since the effective area sampled for males is larger than that sampled for females, since males are more mobile, therefore the MMDM was likely to be inflated by the male bias. Wilson & Anderson's (1985) study, to estimate the effective sampling area of rodent trapping grids, implicitly assumed that the MMDM comes from a single distribution. Most density estimates of big cats based on camera trap records, now use a single MMDM to calculate the effective sampling area, using the method first employed by Karanth & Nichols (1998) for their estimates of tiger density. This may not give an accurate density estimate since, as this study has shown, MMDM differs between male and female jaguars. Further study of the effects of the extreme dichotomies in MMDM within populations on effective sampling area, thus density estimates, would be prudent and would allow accurate estimates of density of the sex with low capture rates.

The male jaguars in this study showed no sign of territoriality. More than one individual occupied the same location. There was no evidence that any one individual was captured more frequently than any of the other males occupying the same location. Neither was there any evidence that male jaguars avoid one another. It is possible that certain individuals are dominant in the area but other males are tolerated up to a certain level. Spatio-temporal avoidance has been demonstrated between jaguars and pumas indicating that the method of using cameras can detect such differences (see Chapter 6). Spatial distribution patterns showed that individual jaguars did keep to particular ranges over the years. Disappearance of a male was followed by increased activity as neighbouring males moved into the vacated area (Appendix B). Overall this suggests loose home range use by male jaguars with extensive range overlap between the individuals. Telemetry data described a similar pattern for jaguars (Rabinowitz & Nottingham 1986) noting a large level of overlap with similar shifts following the death of a male. This is indirect evidence that camera trap data gives accurate information on spatio-temporal distribution. There was extensive overlap in female ranges but the number of female jaguar captures in this study was too low to draw conclusions about female territoriality.

The difference in ranging behaviour between the two sexes is usually explained in terms of each sex optimising access to different limiting resources. Females in polygamous mating systems with females as the sole provider for young, maximise access to food for raising cubs whilst males require larger ranges in order to maximise access to females for mating opportunities (see Chapter 1, Clutton-Brock 1989). The processes underlying the extensive overlap in male ranges are not clear. Most theoretical models of big cat spatial distribution are of exclusive home ranges (See Chapter 1). Rabinowitz & Nottingham (1986) suggested that large trails are a scarce resource in the dense secondary forest of the CBWS and multiple jaguars use them as easy travel routes, resulting in extensive range overlap. The dense vegetation of the CBWS is uniform and lacks natural boundaries which could be used as accessible travel ways such as clearings with forest edge or distinct large river systems (rather the whole area is covered by streams). Territorial defence may be difficult in such a habitat for the defender may not be able to anticipate the location of incursions by potential competitors.

Alternatively (or additionally) the relatively high density at which jaguars live in the CBWS (see Chapter 3) may cause a breakdown of the strict territorial system such that the ranges overlap. High jaguar abundance implies adequate food availability. Rabinowitz & Nottingham (1986) found that armadillos (*Dasypus novemcinctus*) were the main jaguar prey, and they remained so during the present study together with pacas (*Agouti paca*, see Chapter 8). Both prey species are relatively small ( < 6 kg) and can reach high abundances, distributed relatively evenly across an area (Beck-King at al.1999). High abundance and even distribution of prey may facilitate hunting however the small size of each prey item would necessitate frequent hunting to satisfy the jaguars' energetic needs. In such a scenario there would be less time for territorial defence while the high prey abundance would make defence unnecessarily costly and several individuals could hunt in close proximity. Reliance on larger prey species, such as peccary or deer, gives a different scenario. Larger prey species will naturally exist at lower densities with consequentially higher search and handling times but also higher energetic gain from a single hunt. A single carcass of a larger deer or a peccary will provide food for several days. In such a scenario the jaguar would have more 'free time' when in possession of a carcass but would be more food stressed when searching and hunting for prey. Search time would be increased if conspecifics are hunting in the same area since they will lower the local prey population and increase prey vigilance (larger prey have larger home ranges, meaning that nearby conspecifics hunt the same prey individuals). In this situation territorial defence could pay-off. Further study of jaguar social system in relation to jaguar density and prey species is necessary to test these hypotheses.

There was no evidence that males actively search for females throughout the year. Female jaguars are only in oestrus for about 7 days (Kitchener 1991). Males may monitor the status of females by regularly checking scent marks left by females but this behaviour does not require active search in close proximity to the female (see Chapters 1 and 9). Males and females were captured more often on the same day at the same location than were different males. Same-day captures can probably be attributed to active pursuit of oestrus females by males. Two accounts during the 4-year study period could be interpreted as mating events. In the first, a female and a male were repeatedly captured on the same trail over a period of 2 days (8 male captures and 5 female captures). There were no dual captures but the time between captures was low. In the second account a male-female pair was captured over a period of one night (8/12 captures were of both individuals together). Jaguar calls were heard that night. The individuals in both accounts were adults that had been captured in previous years, the pairs could not be mistaken for a mother with an older male juvenile.

Some camera locations were altered between the five annual surveys used for the open population analysis. Changes in camera location from year to year can alter the overall trap success of the survey and so inflate the variation in abundance estimates between the years (Chapter 3). Variable trap success from year to year, due to changes in the camera locations, may influence open population model estimates of survival, emigration and immigration. Many individuals would be excluded if data from cameras with altered locations were eliminated from the analysis; therefore data from every main survey camera were included in the open population analysis to estimate the life history parameters. It is assumed that the effect of altered camera location, thus trap success, between the years is marginal: Between 2002 and 2003, five camera locations were altered but only two new individuals were captured in 2003 (see Chapter 2 and 3). After the 2003 survey a single camera was moved, subsequently 7 new individuals were captured at the new location in 2004. This probably reflects immigration rather than increased trap success since only two individuals were captured there during the 2005. Also the wet season survey of 2003 only captured two individuals at this location (see Chapter 4).

The most parsimonious open population model was of a stable jaguar population of ~12 individuals in the study area, corroborating that the original premise of Chapter 3, of no change in the population between years. In this model the higher number of individuals captured in 2004 and 2005 were attributed to temporary immigration. A jaguar population of ~12 individuals is closest to the estimates of 2002 (14) and 2003 (10) which corroborates the finding that abundance was grossly overestimated for 2004 (35) and 2005 (21). The high immigration and emigration estimates could indicate that the survey area was too small to accurately estimate abundance. Many individuals moved in and out of the area. It is likely that only those individuals occupying the core of the survey area were reliably sampled each year. The high level of immigration corroborates the findings of a highly mobile male jaguar population with fluctuating occupancy.

Survival throughout the 5-year period was estimated at 100%. This estimate was probably inflated by the recapture of a male jaguar in 2006 which had been absent since 2002. His emigration and subsequent return means that it is impossible to distinguish the disappearances of M00-1 and M02-6 as emigration versus mortality. Indeed the disappearance of M02-4 after 2004 was attributed to death until he was recently captured in late 2006 (pers. comm., R. Foster, PhD student, Southampton University). The high mobility of males and the fact that an individual moved out of the survey area and returned after several years indicates that reliable estimates of life history parameters will require either survey areas to be larger than that used in this study (+200 km$^2$) and/or that the annual surveys are continued for several years to cover the turnover of at least one cohort.

## Conclusions and recommendations

Reliable estimates of life history parameters of jaguars inhabiting the secondary forest of Belize will require more than 5 years of data and ideally survey areas > 200 km$^2$ in order to sufficiently sample the population. Sexual differences in capture rate and mobility were identified within the study population. This is likely to be reflective of large cat species in general. Capture rate heterogeneity within the population can inflate abundance estimates (Chapter 3) and this chapter shows that this might be a structural problem embedded in the social system of cats. It is also recommended that further investigation is made into the effect of dichotomies in mobility on density estimates if MMDM is used to estimate effective sampling area.

This chapter demonstrates that camera trap data can be used to test ecological hypotheses. Camera trapping allows the study of interactions between individuals with much larger sample size of individuals and data points than telemetry would be able to acquire at similar cost. The present study should be used as a template for future camera trap studies on spatial distribution patterns of jaguars. The social system of jaguars in the study area seems to be plastic, with extensive range overlap between males and females. It is not clear what drives such a social system. It maybe related to density. A meta-analysis of the combination of abundance estimates and spatial and temporal distribution patterns from camera trap data across the jaguar range would give useful information on the relationship between density and the social systems of jaguars. Study of diet in these areas will give extra information on potential processes driving the different social systems.

The unique situation that both abundance and spatial questions can be tackled with the same methodology gives the opportunity to study other cryptic species more in depth than ever before. In Chapter 6 the spatial and temporal distribution of jaguars will be studied in relation to the distribution of the sympatric puma. Success of such studies will encourage long term research with the potential for repeated surveys and multiple open population model analyses.

# Chapter 6

# Spatial and temporal distribution patterns of jaguars compared to pumas

## Abstract

Jaguars and pumas were studied in the dense secondary forest of the Cockscomb Basin Wildlife Sanctuary (CBWS), Belize. It was shown that both jaguars and pumas were predominantly nocturnal and had substantial spatial overlap but avoided occupying the same space at the same time. Other studies have only compared attraction and avoidance between jaguars and pumas, but the study of avoidance requires calibrating interspecific interaction against intraspecific interactions. This study shows that jaguars and pumas avoid each other more than they avoid conspecifics. In addition it was found that jaguars leave forest trails more readily than pumas. This study is the first time that camera trap technology has been used to answer questions about the mechanisms of coexistence of two highly cryptic sympatric species, the jaguar and the puma, in terms of spatial and temporal distribution.

## Introduction

The long-term persistence of a carnivore species cannot be assessed in isolation from other species, particularly its potential prey and its potential competitors. The availability of prey is the most important factor influencing the survival of large felids, more so than direct persecution (Chapter 1). This is further complicated by competition with other predators for this resource. Exploitation of common resources can occur with or without direct interference between species. Exploitative interspecific competition between two species lowers the carrying capacity of both species and competition can be so strong that it causes the exclusion of one species at the cost of the other (Begon et al. 1996; Tokeshi 1999). Around the world predators avoid high levels of interspecific competition via mechanisms that reduce niche overlap.

A good example of two carnivores with potentially high niche overlap is the jaguar and puma. The range of the jaguar completely overlaps with the range of the puma throughout Latin America, while the range of puma is larger, extending further into North America, the Andes and to the tip of South America. The mechanisms by which they avoid direct competition are not clear. The aim of this chapter is to study the mechanisms of coexistence of the two largest sympatric felids in the neotropics, the jaguar and the puma.

The spatiotemporal distribution of jaguars and pumas is examined in this study. Three years of camera trap data are used to compare the activity and ranging patterns of both species. This provides insight into the coexistence of species with extensive niche overlap. Understanding jaguar and puma coexistence is vital for their conservation. It will allow assessment of the likely impact of environmental degradation on the two species and whether the balance will shift, favouring one species over the other, as habitat is fragmented and prey species are depleted by humans.

Several mechanisms have been described in large carnivores which reduce direct competition for prey:

1) Differentiation in choice of prey size: for example tigers (± 200 kg), leopards (± 45 kg) and dholes (± 15 kg) in Nagarahole, India focus on different size prey species (Karanth & Sunquist 1995; Karanth & Sunquist 2000). The heavier tiger focuses on large bovines and larger deer species while the leopard and the group hunting dholes hunt for the medium to small size deer.

2) Different activity patterns: for example dholes and leopards in Nagarahole, India are diurnal and nocturnal respectively and timing of hunting does not overlap (Karanth & Sunquist 2000).

3) Differentiation in habitat use: for example, leopards make more use of close woodland patches while tigers use the more open grasslands in Chitawan National park, Nepal (Seidensticker 1976).

4) Spatial avoidance: for example cheetahs avoid areas with high prey densities that also support high densities of lions and hyaenas in the Serengeti in Tanzania (Durant 1998).

These four mechanisms allow the coexistence of large carnivores but may often involve the subordinate species utilising less preferred prey, hunting times or hunting areas than the dominant species. Dominance is maintained by the larger carnivore species if it can easily kill the smaller species; for example tigers can kill leopards, and lions can kill cheetahs. The mechanisms of coexistence of jaguars and pumas in the neotropics are less obvious. Although the jaguar is heavier and more bulky than the puma there is considerable overlap between the species (female jaguars may be smaller than male pumas, Chapter 1). Since both species are of similar size they can easily tackle all the available prey species, and potentially each other.

Dissimilar activity patterns have been proposed by many authors as a potential mechanism by which larger carnivores avoid direct competition (Bertram 1979, Konecny 1990, Kitchener 1991, Durant 1998, Karanth & Sunquist 2000). Telemetry in Belize and a camera trap study in the Bolivian Chaco showed that jaguars are predominantly nocturnal in these areas (Rabinowitz & Nottingham 1986, Maffei et al. 2004). Telemetry of jaguars and pumas in the Venezuelan Llanos indicated that both species are mainly active at night. Both were also active during the day and the activity patterns for both species were similar (Scognamillo et al.2003). In the present study camera trap records of jaguars and pumas are used to test the hypotheses that daily activity patterns are similar between the two species, both across the seasons and between years. Van Schaik &Griffith (1996) were the first to use camera trap records to study the activity patterns of rainforest vertebrates. This present study follows their assumption that the relationship between capture frequency and activity is constant throughout the day and night.

No evidence was found for habitat differentiation by jaguars and pumas in Belize based on capture frequency in locations differing in slope, altitude or distance to rivers (see Chapter 4). Similarly Scognamillo et al. (2003) found no difference in habitat use between jaguars and puma in the Venezuelan Llanos. It is unlikely that habitat differentiation is an important mechanism of competition avoidance between jaguars and pumas, particularly in the homogeneous environment of Belizean rainforest.

Lack of habitat differentiation does not signify that jaguars and pumas do not avoid each other in space. They may use similar habitats but in different locations. In this study the hypothesis that the two cats avoid each other in space is tested by comparing capture frequencies of the two species at every camera location.

Avoidance may have both a spatial and a temporal component; for example although there was high overlap in habitat use and activity patterns of jaguars and pumas in the Venezuelan Llanos, the two species did not occupy the same space at the same time (Scognamillo et al. 2003). In the present study analysis of temporal avoidance, based on activity patterns, is combined with analysis of spatial avoidance, based on capture locations, to test the hypothesis that jaguars and pumas avoid occupying the same area at the same time. The avoidance or indifference of the two species is further studied by examining the temporal distribution of both species at single camera locations. It was hypothesised that consecutive captures of the same species should be shorter than consecutive captures of two different species indicating avoidance between the species, and that captures of the same species should be clustered through time, indicating interspecific avoidance compared to intraspecific avoidance.

The success of one species over a potential competitor can be estimated from data on relative abundances as proportions of intrinsic carrying capacity. Núñez et al. (2002) used telemetry to estimate and compare densities of jaguars and pumas in the dry seasonal forest of Jalisco, Mexico. In this area, which is not representative of jaguar habitat in general, pumas were more abundant with 3.5 pumas/100 km$^2$ compared to just 1.7 jaguars/100 km$^2$. This suggests competitive dominance of pumas, if both species have similar carrying capacities in the absence of the other. Camera trap data have been used to estimate the jaguar abundance of the CBWS in Belize at a conservative estimate of ~10/100 km$^2$ (see Chapters 3 and 4). It was not possible to estimate puma abundance in this study because they cannot be individually identified (see Chapter 2). Any comparison between jaguars and pumas has to be based on capture frequency. Capture frequency cannot be used as a measure of relative abundance. To do this would assume that their use of the forest matrix is similar, in particular to their use of trails. Trail systems are the most successful capture sites for both jaguars and pumas in secondary forest (see Chapter 4) but they may have differential importance for the two species. Intensive trail use may indicate a high dependency on trails for hunting and travelling and the availability of trails may be a limiting factor in the distribution of the species. The stocky build of jaguars is likely to be better suited to the dense forest environment than is the slender and long-limbed body of pumas, and so it was hypothesised that jaguars will be more likely to walk off-trail than pumas. This hypothesis was tested by comparing consistency of trail use between the two species. Consistency of trail use was assessed from the number of consecutive captures along trails.

The objectives of this chapter are:

1) To compare the activity patterns of jaguars and pumas based on the time of capture on camera traps.

2) To examine similarity in the spatial occupancy of the two cats in terms of capture rates at the different camera locations.

3) To study attraction or avoidance between the two cats by comparing inter- and intraspecific time differences between captures on similar cameras.

4) To compare the use of trails between the two cats by examining the number of consecutive cameras triggered or missed along single trails.

# Methods

Jaguar captures were biased towards males (Chapter 5), therefore puma sex ratio was calculated before comparing puma and jaguar capture frequencies. Sexing pumas was difficult due to the lack of individual recognition. The sex ratio of known sex pumas was calculated and compared with the jaguar sex ratio.

## *Activity patterns of jaguars and pumas*

The general activity patterns of jaguars and pumas were deduced from the photo records. The time when the photograph was taken was used to create a 24-hour activity pattern for both species. The number of photographs was summed within each hour for all the captures of the survey (00:00 to 00:59; 01:00 to 01:59; 02:00 to 02:59 etc). To avoid bias caused by multiple captures of the same individual within the same hour by one or several neighbouring cameras each individual was only counted once within any hour on each day. The activity patterns were converted to percentage of captures within an hour to make comparison possible between the two species. A Pearson correlation of percentage of jaguar captures in each hour and percentage of puma captures in each hour was calculated to test the hypothesis that jaguars and pumas have similar activity patterns. The percentage data were arcsin transformed. Activity patterns were calculated separately for jaguar and puma captures during the dry season and the wet season and for captures in the years 2003 and 2004. The hypotheses that neither jaguar nor puma activity patterns vary between the dry season and the wet season or between the years were tested by calculating Pearson correlations of each relationship.

## *Spatial overlap between jaguars and pumas*

To evaluate spatial overlap between jaguars and pumas, Pearson correlations were calculated for the log10 captures or captures rates of both cats (Minitab version 14):

The first correlation examined the overlap in capture numbers between jaguar and pumas for the 13 surveys to examine similarity in capture frequency for the different areas.

The second correlation examined the similarity between the two cats in number of captures at every camera location through the entire study period, to test the hypothesis that there is spatial overlap between jaguars and pumas. A negative correlation was expected if jaguars and pumas do not use the same areas, whilst a positive correlation would indicate spatial overlap between the two species.

The third correlation examined the similarity between the two cats in number of captures at every camera location per calendar month, hereafter called camera-month, to study whether the spatial distribution of jaguars and pumas varied through time. Percent captures per camera-month were calculated for all camera-months with $\geq 25$ trap nights. A positive correlation was expected in case they are attracted and a negative correlation if they avoid one another. Different camera locations were active for periods of 2 to 20 months therefore longer running camera locations contributed more data points to the analysis than did camera locations that were active for fewer months. To account for the non-independence of the data points Pearson correlations of puma and jaguar capture rates per calendar month were calculated separately for the all camera locations that had records $> 2$ months. These correlations were compared to the full correlation to determine whether the contribution of the long running cameras biased the results.

## *Temporal avoidance between jaguars and pumas*

Temporal avoidance of jaguars and pumas was analysed in more detail by comparing the number of days between jaguar-jaguar captures, puma-puma captures, jaguar-puma captures and puma-jaguar captures. A General Linear Model (GLM) analysis was used to test whether the number of days between the first capture and the consecutive capture differed significantly, using species (jaguar or puma) as the main factor for the first capture and the consecutive capture. The GLM was used to test the difference between same species (main effects) and between different species (interaction effect):

Number of days between captures = Capture1 | Capture2 + $\varepsilon$

with Capture 1 and Capture 2 each having 2 levels: jaguar and puma.

The data were log10 transformed to approximate a normal distribution of the residuals. It was hypothesised that jaguars and pumas avoid each other through time such that the time between jaguar-puma captures and puma-jaguar captures would be significantly longer than between jaguar-jaguar captures or puma-puma captures. No difference was expected in number of days between jaguar-jaguar captures and puma-puma captures (the main effects).

If jaguars and pumas avoid each other then it is expected that captures are clustered for each species in time. A non-parametric runs test was used to test the hypothesis that the temporal distribution of the two cats at each camera location differed from a random distribution. The number of runs of consecutive captures of the same species through time indicates to what extent the species avoid each other. Fewer runs than expected from random, i.e. a clustered distribution of same species captures, indicates that jaguar-jaguar captures and puma-puma captures are more common than puma-jaguar captures or jaguar-puma captures. This in turn would imply that the two species avoid each other. Data were only used from camera locations with a minimum of three captures for each species. The sample sizes were too low to perform the runs test separately for each camera location so the data from 22 camera locations were pooled. The runs test was performed on this pooled data set of 853 jaguar and puma captures.

## Trail use by jaguars and pumas

Trail use by jaguars and pumas was investigated using data from cameras located at regular intervals along single trails. It was hypothesised that pumas follow trails more frequently than jaguars. The number of 'walks" along a trail was used as an index of how frequently either species followed trails. A "walk" was classified as $\geq$ 2 captures of the same individual at different locations along a single trail within 1-2 hours (depending on the distance between locations). The number of jaguar walks and puma walks were calculated using data from 8 different trails. All trails used had records of both jaguars and pumas. Calculation of the number of walks required individual recognition of both jaguars and pumas. Although pumas do not have individually unique coat patterns, recognition of individual pumas is possible in the short-term if they possess visible parasites, wounds or scars (see Chapter 2). For this analysis data were only used for pumas of confirmed identity, which may mean that the number of puma walks is underestimated.

It was further hypothesised that jaguars are more likely to leave a trail to enter the forest during a walk than are pumas. The number of cameras triggered during each walk was used to index trail use, and the number of omissions of cameras during each walk was used to index walking off-trail. Camera failure was assumed to be similar for both species (both same size and height). Difference in trail use, and the difference in walking off-trail between jaguars and pumas was tested using Student *t*-test. The data were log10 transformed to approximate normal distribution.

## Results

The sex ratio of pumas was just as skewed towards males as it was for jaguars: of the 608 puma capture events, 409 were males and 37 were females (162 were unknown). The capture events ratio for known sexed jaguars was 575 males and 59 females. $\chi^2$ test between the known male:female sex ratio of both species indicated no difference ($X^2 = 0.33$, d.f. = 1, $p = 0.57$) warranting comparison between puma and jaguar captures.

### *Activity pattern of jaguars and pumas*

The activity patterns for both jaguars and pumas were similar (Figure 6.1). There was a high degree of overlap between the patterns of activity of jaguars and pumas per hour (Pearson correlation $r = 0.69, p < 0.01$ for the arcsin transformed data). The activity patterns of subsets of captures from jaguars and of pumas were positively correlated between the wet and dry seasons, and between the years 2003 and 2004 for each species (Table 6.1). This shows that the activity patterns of jaguars and pumas remained stable between the seasons and years.

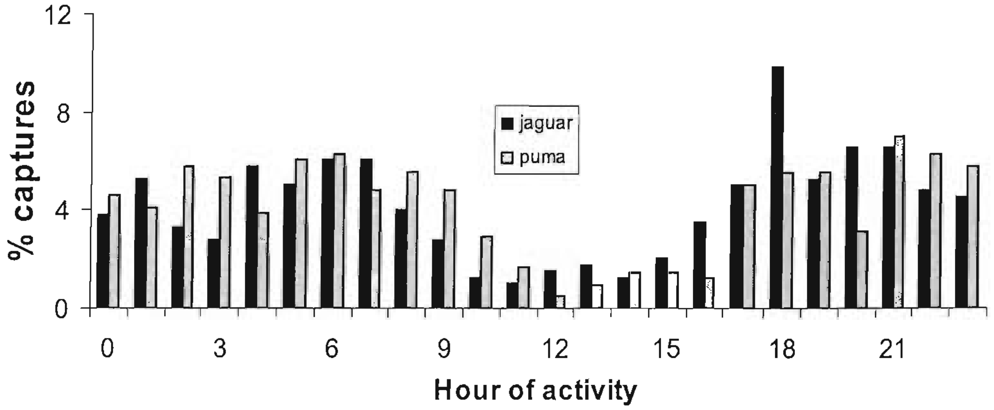

Figure 6.1 Percentage of jaguar and puma captures per hour (*N* jaguar = 397, *N* puma = 413).

Table 6.1 Pearson correlations for hourly activity patterns (as in figure 6.1) across seasons and years.

| Species | Comparison | Correlation | *p*-value | *N* captures used for % calculation | |
|---|---|---|---|---|---|
| **Jaguar** | **dry-wet** | 0.47 | 0.02 | dry = 253 | wet = 80 |
| **Puma** | **dry-wet** | 0.73 | 0.00 | dry = 210 | wet = 144 |
| **Jaguar** | **2003-2004** | 0.55 | 0.01 | 2003 = 103 | 2004 = 150 |
| **Puma** | **2003-2004** | 0.65 | 0.00 | 2003 = 149 | 2004 = 195 |

## *Spatial overlap between jaguars and pumas*

The total number of captures of jaguars and pumas for each survey were similar and positively correlated (Pearson correlation 0.69 for log10 captures, $p < 0.01$, $N = 13$, Appendix D, Table D.9). There are two notable outliers: three times as many puma as jaguar captures on the western trail during the "scrape 2003" survey and three times as many jaguar as puma captures along the CBWS access road during the "access road" survey. The western trail is a disused logging road through the forest, whilst the access road has frequent vehicle traffic in and out of CBWS.

Pumas had similar levels of occupancy as jaguars at each camera location: the total log10 number of jaguar captures at each camera location was significantly positively correlated with the total log10 number of puma captures (Figure 6.2a).

Jaguar and puma capture rates per camera-month did not show this relationship. There was no significant correlation between puma and jaguar capture rates (Figure 6.2b). Within any given month jaguars and pumas did not have similar levels of occupancy at a given location. There were no instances of high numbers of jaguars and high numbers of pumas occurring together at the same place and at the same time (upper right of the distribution). This suggests the possibility of an inverse relationship of the sort jaguar × puma = constant. However log10 (month/jaguar) did not correlate with log10 (puma/month): $r = 0.08, p = 0.35$. The capture rates per month were uncorrelated but not simultaneously high in general. Within camera correlations ranged from $-0.8 < r < 0.5$, indicating no fixed relation between capture rates at any given location.

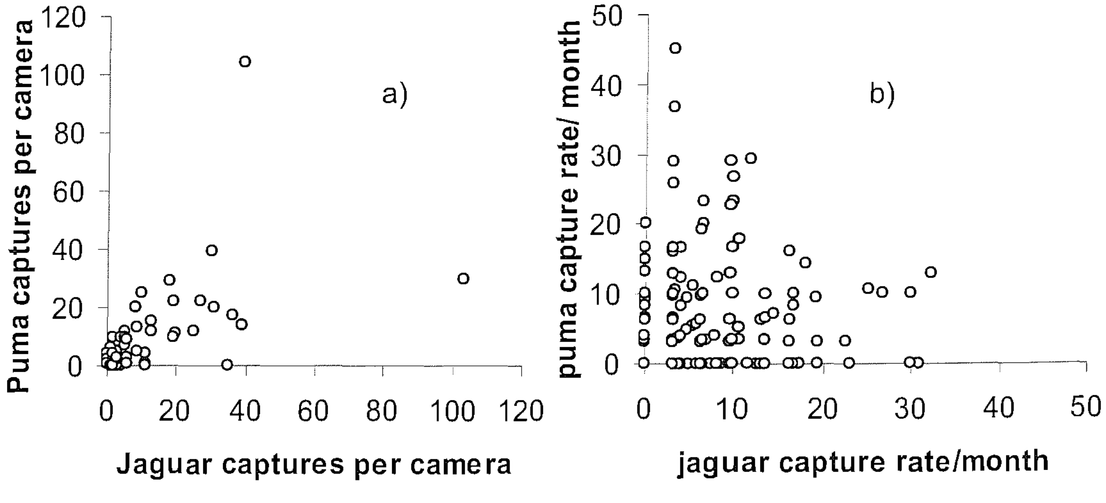

Figure 6.2 a) Scatter plot between jaguar captures and puma captures at each camera location ($r = 0.65$ between log10 captures, $p < 0.01$, $N = 93$). b) Jaguar and puma capture rate per camera-month (Pearson correlation between log10 non zero captures, $r = 0.09$, $p = 0.17$, $N = 258$).

## *Temporal avoidance between jaguars and pumas*

The time interval between consecutive jaguar captures was not significantly different than the time interval between consecutive puma captures (Table 6.2, $p = 0.68$, $p = 0.74$). The time interval between jaguar-puma captures and puma-jaguar captures was significantly longer than the time interval between consecutive single species captures ($p < 0.01$: Table 6.2 and Figure 6.3). This indicated that jaguars and pumas avoided each other in time.

Table 6.2 Balanced ANOVA on time interval between consecutive captures (each with jaguar and puma as the two factor levels). The data were based on 278 jaguar to jaguar captures, 258 puma to puma captures, 166 jaguar to puma captures and 173 puma to jaguar captures.

| | d.f. | SS | MS | *F*-value | *p*-value |
|---|---|---|---|---|---|
| **Capture 1** | 1 | 10.60 | 10.27 | 0.17 | 0.68 |
| **Capture 2** | 1 | 6.45 | 6.63 | 0.11 | 0.74 |
| **Capture 1 * Capture 2** | 1 | 393.95 | 393.95 | 6.59 | 0.01 |
| **Error** | 871 | 52038.14 | 59.75 | | |
| **Total** | 874 | 52449.15 | | | |

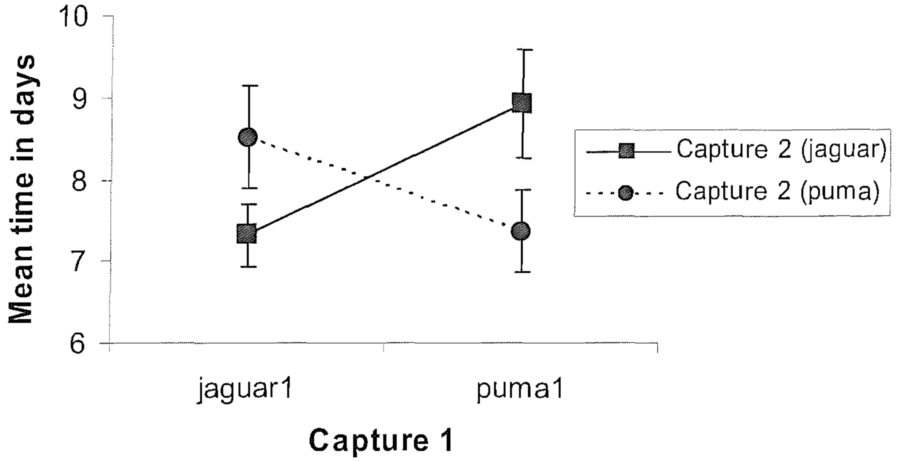

Figure 6.3 The mean of number of days between consecutive photographic captures on single cameras. The x-axis shows the species for the first capture and the legend shows the symbol for the species of the second capture.

The order in which jaguars and pumas were captured through time differed significantly from random (373 runs of consecutive puma or jaguar captures observed, 427 expected, average $K = 0.52, p < 0.01$, Appendix D: Table D.10). The number of observed runs was significantly lower than the expected number of runs, indicating that the jaguar and puma captures were both clustered. This indicates that the two species avoided each other.

### *Trail use by jaguars and pumas*

Pumas walked trails more frequently than did jaguars: 70 puma walks and 44 jaguar walks were recorded throughout the 3-year study period. The number of consecutive cameras triggered by jaguars along single trails was significantly lower than by pumas (mean number of cameras 3.2 and 3.6 respectively, $t_{110} = -2.65$, $p < 0.01$, Appendix D: Table D.11), whilst the number of omissions of captures along single trails was significantly higher for jaguars than for pumas (mean number of cameras 0.3 and 0.1 respectively, $t_{56} = 2.79$, $p < 0.01$, Appendix D: Table D.11). These results show that pumas tended to remain walking along the trail during a single bout of activity whilst jaguars were more likely to make excursions on and off the trail.

## Discussion

Studies of carnivore coexistence tend to focus on species for which mechanisms of avoiding competition are obvious, such as those with a distinct size difference (e.g. Karanth & Sunquist 1995 with tigers and leopards). Here 3 years of camera trap records of jaguars and pumas have provided an ideal opportunity to study the coexistence of two carnivores with extreme niche overlap.

The similarity of jaguars and pumas in body size (Chapter 1), habitat use (Chapter 4; Scognamillo et al. 2003) and potential prey species (Chapter 7) means that the mechanisms of coexistence are not clear. This study found no evidence to suggest that jaguars and pumas avoided direct competition by being active at different times of the day, (as found for other carnivores; Bertram 1979, Konecny 1990, Kitchener 1991, Durant 1998, Fedriana et al. 1999, Karanth & Sunquist 2000), or that the two species have spatially explicit ranges (as found for other carnivores; Seidensticker 1976, Fedriana et al. 1999); however it did show that within their overlapping ranges jaguars and pumas avoided one another through time. These findings are consistent with Scognamillo et al's 2003 study of jaguars and pumas in Venezuelan floodplains. However they only made comparison between the two species, not within each species. Within species comparisons are also necessary in order to show whether interspecific avoidance is greater then intraspecific avoidance. The present study specifically demonstrates that jaguars and pumas avoided each other more than they avoided conspecifics. The difference in habitat between the Venezuelan floodplains and the rainforest in Belize can be used as evidence for a more general model of jaguar and puma coexistence in which the two cat species have highly overlapping ranges and activity but avoid interspecific competition by occupying different areas of their ranges at different times. This means that jaguars and pumas are ecologically more similar than other carnivores of contemporary coexistence studies. The close similarity of between the two cats stimulates questions about the limits of carnivore coexistence. The mechanisms of coexistence of jaguars and pumas may be more subtle than those previously described in other sympatric carnivores.

Differential use of trails may also reduce direct competition between the species. Jaguars leave trails more frequently than do pumas. They may be better adapted to travel or hunt in the dense secondary forest than are pumas. Certainly their build would suggest this. The intense use of trails by pumas may indicate that they use trails more frequently for hunting while jaguars use the trails intermittently as short cuts for traversing the forest. Such niche separation could provide a mechanism for coexistence in which jaguars are specialist hunters of dense forest and pumas hunt in more open areas, which coincides with the mechanism of coexistence by differential use of space (Durant 1998, Fedriana et al. 1999). Different prey species utilise trails to different extents (Chapter 7) so differences in hunting strategy may be detected in differences in diet between the species (Chapter 8) as found for other carnivores (Bertram 1982, Karanth & Sunquist 1995; Karanth & Sunquist 2000). Subtle habitat separation and associated diet differences could be the main mechanism by which jaguars and pumas are able to coexist. Such a mechanism would result in a higher abundance of jaguars in closed areas and higher abundance of pumas in open areas. In conservation terms this would mean that dense rainforest would suit jaguars better than pumas. Removal of primary forest and regeneration of forest through a secondary growth forest would favour the jaguar even more than the puma. Extensive removal of forest with the creation of open patches would suit pumas better than jaguars. The ratio of jaguar abundance to puma abundance needs to be better understood in different habitats in order to predict the likely impact on either species in the face of environmental changes

No conclusions can be drawn about the dominance of jaguars versus pumas in the CBWS. Although the data showed that jaguars and pumas do avoid one another it was not possible to distinguish whether one species was subordinate and actively avoided the more dominant species. Nor could any conclusions be drawn about the success of jaguars versus pumas since abundance estimates of pumas were not possible. The differential trail use by both species shows that relative abundance indices based on capture rate will be biased towards pumas by an unknown factor if camera traps are mainly located on trails. Puma abundance could not be quantified in this study. Jaguars tend to walk off trail more frequently than did pumas but the capture rates of pumas and jaguars on trails were similar. This implies that the abundance of jaguars in the CBWS is higher than the abundance of pumas. Further anecdotal evidence based on camera trap data over short intervals of ~3 weeks in small areas (~5 camera locations) suggested that fewer puma individuals were present than jaguar individuals. Further study of the coexistence of jaguars and pumas requires the development of methods to estimate abundance of pumas such as mark-recapture analysis using genetic samples (scats or hairs). The high level of overlap in activity patterns and use of space means that it is important to understand the dietary overlap between the two species. For this reason the diet, based on scat data, was compared between the two species in Chapter 8.

# Chapter 7

# Estimation of prey abundance in the Neotropics

## Abstract

One of the major conservation concerns for endangered carnivores is the availability of prey. Knowledge of abundance of major prey species is necessary to accurately predict the viability of carnivore populations. Such knowledge is deficient in tropical environments due to the lack of accurate methodologies to measure prey abundances. In this chapter the use of camera traps is studied as a potential means to estimate abundance of prey species of jaguars and pumas in Belize. Sign surveys and camera traps were used to estimate the level of trail use by different prey species. It was found that many prey species were caught on camera. There were large differences between species, however, in their extent of trail walking and probability of triggering cameras. It was concluded that care should be taken when using camera traps to compare abundance indices between prey species due to the biases inherent in the method.

Activity patterns of the prey species, derived from camera trap data, were compared with the activity patterns of jaguars and pumas. Most major prey species were diurnal while jaguars and pumas were mainly nocturnal. Evidence was found that both jaguars and pumas are attracted to white-lipped peccaries (Dycotylis pecari) but that the relation is much stronger for pumas than for jaguars.

## Introduction

One of the most important variables for the survival and reproductive success of an individual is availability of food. Other variables can be limiting factors for an individual, such as nesting sites or suitable habitat but food is a factor that can regulate population size most profoundly. This is especially true for carnivores due to their position at the apex of the food chain. The density of tigers has a strong positive relation with prey density (Chapter 1). The reduction in numbers of prey, rather than direct persecution, was the main threat to long-term tiger survival. Monitoring prey numbers of tigers' preferred prey species in key areas was considered more important for tiger conservation, than monitoring tiger populations themselves (Karanth & Stith 1999). Reduction in prey populations can occur rapidly in the face of human hunting pressure, and carrying capacities of carnivores can be reduced before the numbers of carnivores have adjusted. Knowledge of the density of prey species could give information on the carrying capacity of a predator population in the absence of knowledge of the predators' abundance. The aim of this chapter is to examine prey availability for the two largest Neotropical felids, the jaguar and puma.

Predator-prey relations of the more easily observed larger carnivores have been relatively well studied, for example those that live in open savannah and open woodland areas such as tigers and lions (Sunquist et al. 1999, Hayward & Kerley 2005). Knowledge of predator-prey dynamics are lacking for carnivores that live in densely forested areas. The present overexploitation of bush meat in African rainforests exemplifies the need for such data and its effect on tropical African carnivores (de Merode & Cowlishaw 2006, Fa et al. 2000). Such studies base abundance estimates on the availability of bush meat in markets rather than on the wild populations.

The effect of bush meat extraction has received less attention in the neotropics. Hunting is a potential threat to the prey of neotropical carnivores (Novack et al. 2005, Franzen 2006, Cullen et al. 2001). Few data exist on prey availability for the neotropical jaguar and puma. Several studies have described jaguar and puma diet in different parts of their range (Rabinowitz & Nottingham 1986, Núñez et al. 2000, Novack et al. 2005, Taber et al. 1997, Scognamillo et al. 2003, Emmons 1987, Crawshaw & Quigley 2002, Leite & Galvão 2002.). Diet will be analysed in detail in Chapter 8, but lack of reliable methodology has hindered collection of information on prey availability. In this Chapter the efficacy of several methods of prey abundance estimation were tested and reviewed for use in densely forested areas, highlighting the potential for camera traps to be used to estimate prey density in neotropical secondary forests.

Estimating mammal abundance in neotropical forests is often difficult due to their low numbers and poor visibility in the dense vegetation of secondary forest (discussed in Chapter 2). Line transects are most frequently used, surveying for sign such as tracks and faecal material of the target species; or distance sampling is used to survey for live animals (Buckland et al. 2001). Such surveys are popular because they are cheap.

Most studies employ line transect sign surveys to compare the relative abundance of target species between neighbouring areas which differ in hunting intensity, extraction of other natural resources or habitat type (Granjon et al. 1996, Peres 1996, Escamilla et al. 2000, Cullen et al. 2001, Reyna-Hurtado & Tanner 2005). The use of relative abundance indices negates the need for absolute abundance estimates. This technique allows within-species comparisons between areas not between-species comparisons. Between-species comparisons require that the signs for the different species sampled have an equal chance of detection. Rabinowitz & Nottingham (1986) used sign surveys to estimate prey species availability in the Cockscomb Basin of Belize. They used transects to survey for a wide variety of mammalian sign but gave no details of the methodology or evaluation of assumptions of equal detection probability between different species. It is unlikely that the sign of different species have the same probability of detection because of the great variation between species in weight (probability of producing footprints), trail use, cryptic behaviour (avoidance of open space, even narrow transect lines) and substrate quality between areas. Conversion of sign-survey data into absolute abundance requires empirical data on the relationship between the number of signs found and the true abundance of the surveyed species. Such data do not exist for neotropical mammals.

Distance sampling (Buckland et al. 2001) is used to estimate absolute abundance based on sighting frequency and distance from the transect line of target species. Many studies have used the technique to estimate densities of species, for example prey species of tigers in India (Karanth & Sunquist 2000), badgers in England (Hounsome et al. 2005), monkeys in tropical African forest (Refish & Kone 2005) and desert animals in Jordan (Scott et al. 2005). Reliable estimates from distance sampling requires a large sample size of observations ($N > 60$, Buckland et al. 2001), which limits the use of the technique to species that are highly visible and present in relatively high numbers. Terrestrial neotropical forest mammals are not encountered in high numbers and the technique is difficult to use within these regions. Novack et al. (2005) used data of live sightings for the estimation of prey density in tropical forest in Guatemala. No details are given on the difficulty of sighting or the openness of the habitat. The presence of white-tail deer (*Odocoileus virginianus*) suggests that the habitat was open or that perhaps transects were biased towards more open areas (for example road verges). Sighting frequencies are generally too low for surveys in the dense vegetation of secondary forest in Belize (pers obs. B. Harmsen, thesis author; pers comm. R. Foster, PhD Southampton University; pers. comm. M Kelly, assistant professor Virginia Technical University; pers. comm. M Weckel, Msc student, Fordham University). Non-systematic interviews with experienced hunters suggest a low encounter rate with prey species in forested areas of Belize (pers. obs. B. J. Harmsen, thesis author). As such distance sampling is a poor method for estimating abundance of prey species in neotropical secondary forests.

The use of camera traps for estimating individually recognisable species such as jaguars has stimulated interest in this technique for estimating density of prey species. Most prey species do not have individually recognisable features and so estimation of absolute abundance is problematic. Carbone et al. (2002) gave evidence that capture rate of tigers could be used as an index for estimating absolute density of tigers if the relationship between tiger density and capture rate was known, and it was suggested that such a relation could be found for prey species as well. In the absence of individual identification, reported estimates have been based on capture rate. For example, O'Brien et al. (2003) found a positive correlation between estimates of the larger prey species of tigers based on distance sampling and on and camera trap capture rate data in the forests of Sumatra. Silveira et al. (2003) noted that camera traps detected all neotropical prey species that were also detected during sign surveys in an open Cerrado area in Brazil. The frequency of sign was much higher than the frequency of captures on cameras. The camera and sign surveys were carried out on the road systems with good substrate for footprints. Weckel et al. (2006) used camera traps to estimate relative abundance for neotropical prey species in Belize.

The use of camera traps to estimate (relative) prey abundance requires equal probability of capture of the different target species if species are to be compared. This assumption was not met for jaguars and pumas in their use of trails (Chapter 6) and so it is unlikely that the widely differing prey species will have equal capture probabilities on trails. Weckel et al. (2006) gives information on capture rate using cameras along different trail systems within the CBWS, main trail, game trail, forest matrix, but combined all the capture records in an overall relative abundance estimate for each species without further investigation into the effects of the stratified sampling. Camera distribution may influence estimates of relative abundance by favouring different species, for example, a survey that only uses camera locations on trails will be biased towards those species that walk more frequently on trails. O'Brien et al. (2003) provided no data regarding the camera trap locations in their study in Sumatra, for example whether the camera traps and sign surveys were on the same pathways. They noted low capture rates on cameras and low detection rates in sign surveys for the prey species and tigers, which could make estimates relatively unreliable.

The species that a camera trap can capture are determined by its height above the ground: too high and smaller species can walk below the sensor; too low and larger species will not be detected, since legs have a lower chance of triggering the sensor than the body. Small species such as pacas and armadillos are not well detected when cameras are set for larger species such as jaguars, peccary and deer. The suitability of a trail to funnel a species past a camera is also influenced by the size of the animal: wide trails that easily funnel larger species past the camera may be avoided by smaller species. For example, Weckel et al. (2006) noted that pacas and armadillos were photographed significantly less frequently on main trails than on narrower game trails.

Comparison between species capture rate using camera traps requires knowledge of the capture probability of different species in different habitat types with different funnels (trail widths). For this study the trail use by prey was studied for several species using a combination of camera trapping and sign surveys. A relationship was sought between capture rates of the different prey species and habitat variables. Particular attention was paid to potential biases when estimating prey abundance in the neotropical secondary forests, in order to contribute to the development of unbiased comparable relative abundance indices.

Even though abundance estimates of prey species based on camera trap data may not yet be perfected, camera trap data can answer other ecological questions about those species captured. In this chapter they are used to investigate activity of both predator and prey in relation to prey choice, and so to explore the complex predator-prey relationships of larger carnivores in the neotropics. Activity patterns derived from camera trapping are assumed not to be biased since it is considered unlikely that species have different activity patterns at different camera locations. The activity patterns of prey species were compared with those of jaguars and pumas (described in Chapter 6). Cats hunt primarily by auditory and visual cues and thus are more likely to detect active prey than inactive prey (Chapter 1). Prey species with activity patterns that overlap with those of jaguars and pumas may therefore be most susceptible to attack. This hypothesis was tested by comparing the activity patterns of prey species with the preference list of prey species for both cats (Chapter 8).

Most of the potential prey species of jaguars and pumas have distinct home ranges for individuals or family groups and are distributed relatively evenly across an area of preferred habitat (Reid 1997). White-lipped peccaries (WL peccary) are an exception, being nomadic and capable of moving across vast areas in large groups of more than a hundred individuals (Peres 1996, Fragroso 1998). They are the most endangered prey species due to hunting by humans (Peres 1996, Fragroso 1998, Cullen et al. 2000). Of all the prey species available in CBWS, the WL peccaries have the heaviest weight per individual - of the two other large prey species, white-tailed deer are not present and tapirs are rarely taken by jaguars (see Chapter 8). Jaguars are probably better suited physically than pumas to deal with the large tusks and muscular bodies of WL peccaries (see Chapter 1). A sudden influx of large groups of WL peccaries through an area would cause a sudden, but short-term, increase in the prey biomass available for jaguars and pumas. For these reasons this Chapter includes a case study on the influence of the presence of WL peccaries on the two cat species in terms of temporal overlap of activity (camera captures). It is hypothesised that the cats will opportunistically switch prey species to maximise their energy intake (biomass gained per single hunting bout). If jaguars and/or pumas have a preference for WL peccaries then their behaviour will be altered by WL peccary presence and they will follow the herds if they are in the area. The study will test the hypothesis that the jaguars and pumas specifically change their hunting strategy in the presence of an increased temporally variable resource such as WL peccaries.

The objectives of this chapter are:

1) To test for a relation between capture rates of different prey species and habitat variables measured around camera traps.

2) To evaluate trail use by the prey species, from a) proportions of footprints that follow or cross trails, and b) comparison of sign surveys to camera captures.

3) To compare activity patterns from camera trap captures between several larger prey species and the two large cat species.

4) To seek evidence that jaguars and pumas following WL peccaries, using time intervals between captures on camera traps.

# Methods

Baseline data are available of the vertebrate species which should be present in Belize and those known to inhabit CBWS. Species assemblage is similar throughout the jaguars' range, South America has greater species diversity than Central America, especially of primates, but there are no additional genuses or larger species that alter the general mammalian assemblage (See Appendix C for all species in Belize > 1 kg). The only major difference across the region is the presence in South America of the capybara: a large (up to 45 kg) group-living (2-20 individuals) semi-aquatic rodent. This species can be an abundant and important prey for jaguars in the regions where it occurs (Chapter 8).

Mega-fauna such as large herds of ungulates, as found in Africa, Asia and North America, are absent in the Americas, except domestic species. The largest potential wild prey species in Central America is the solitary tapir, which is significantly larger than the next heaviest mammal. Two deer species live in Belize; the white-tailed deer is the larger of the two and it lives in small groups confined to open and edge habitat. In contrast the red brocket deer (*Mazama america*) is a solitary, smaller forest species and unlike the white-tailed deer is found in the CBWS. The only large group-living animals within the CBWS are two species of peccary. The larger WL peccary is nomadic and lives in herds up to 200 individuals; the smaller collared peccary (*Tajassu tajacu*) has fixed territories and lives in groups of up to 12 individuals.

The paca is the only Belizean rodent species with a maximum weight of > 10 kg. They are favoured source of bush meat among the local communities but can be abundant in areas with no human disturbance. Pacas are associated with water, territorial and solitary. The only other mammal > 10 kg is the ocelot a solitary cat living at fairly low densities. It is unlikely that it forms an important part of the large cats' diets.

Most prey species have a maximum weight < 10 kg and a large proportion are < 5 kg. These include a wide range of rodents, carnivores and marsupials. The only group-living species weighing <10 kg is the coati (*Nasua narica*). The coati is an edge species but it does live in the CBWS forest, in large family groups. The remainder of the species in Appendix C are solitary. The armadillo is abundant and reproduces quickly. It is relatively slow-moving and noisy when foraging in the undergrowth, making it particularly vulnerable to predation and easy prey for both cats. There are large numbers of terrestrial and arboreal rodent species < 1 kg present in the region, which could potentially be taken as prey.

There are few species of ground-dwelling birds in the neotropics. Great curassow (*Crax rubra*), crested guan (*Penelope purpurascens*) and great tinnamou (*Crypturellus major*) are all pheasant-like birds that spend much time foraging on the ground and are relatively slow to take-off. These birds can live at relatively high densities in areas where they are not hunted by humans (Jones 2004).

Reptiles and fish are included here for completeness but will not be dealt with in this thesis. Diet studies have shown that they form a relatively unimportant part of the diet (Chapter 8). The neotropics are rich in reptiles. Morelet's crocodiles (*Crocodylus moreletii* ) are small and extremely rare in the CBWS. Several large species of non-poisonous snake, small to medium-sized land and river turtles and large lizards and iguanas live in the region that could also be taken as prey. The puma is probably unable to eat turtles but jaguars are known to break open the hard shells (Emmons 1991). There are also abundant large fresh water fish in the CBWS river systems. All statistical analyses in this chapter were performed using Minitab version 14.

## Habitat preference

Spearman correlations were calculated between the capture rates (per 100 trap days) of 8 prey species and the following capture site variables:

1) Trail: width (m), seasonality (3 ranks, 1 = permanent) and age (3 ranks, 1 = old).
2) Habitat: shortest distances to river (km), stream (km), and water (closest of either stream or river), altitude (m) and slope (degrees).
3) Jaguar and puma capture rates (per 100 days).

A stepwise regression was performed separately for each species between the capture rate and continuous capture site variables. All data were log10 transformed to approximate a normal distribution. The default value of alpha level of 0.15 was used for entry and removal of variables. The habitat associations of each prey species were compared with those of jaguars and pumas.

The mean width of trails used and the percentage of captures on the banks of rivers or streams were calculated for each prey species with > 50 captures.

## *Sign surveys*

Frequency of use and direction of travel along trail systems by prey species were analysed from sign survey records along three main trails, and two new trails, cut specifically for this study (Table 7.1). The main trails had sufficient locations of substrate for footprint production. The new trails had fewer locations suitable for footprints due to the high root mass. The trails were slowly walked by two people who scanned for footprints, large cat scrapes and scats from large cats. Faecal material from other species was rarely found and could not be determined to species level. When footprints were encountered the following variables were recorded:

1. Species.
2. Adult/juvenile.
3. Direction (perpendicular to the path or following the path).
4. Number of footprints in a series that likely belonged to one individual.
5. Location of the footprints relative to fixed markers along the trail.

Each trail was surveyed once per week for the duration of survey. Footprints were cleared after identification so they would not be re-counted the following week. It was assumed that the footprints found each week were produced during the previous week.

Table 7.1 Logistic data for five surveys. *N* cameras = Number of cameras along trails, *N* weeks = Number of weeks for the particular survey.

| Trail name | cut/exist. trail | Length trail (m) | *N* cameras | *N* weeks | Start date |
|---|---|---|---|---|---|
| **1** Antelope | existing | 3747 | 3 | 7 | 29-Dec-03 |
| **2** Juan Branch | existing | 3860 | 12 | 5 | 13-Jan-04 |
| **3** Mexican Branch | existing | 2324 | 20 | 6 | 01-Jun-04 |
| **4** 6K line | cut | 1721 | 19 | 9 | 22-Jul-04 |
| **5** Mitchell Creek | cut | 2594 | 19 | 5 | 22-Dec-04 |

The total number of sets of footprint for each species was summed over all the surveys. The percentage of footprints following a trail and those crossing a trail were calculated for each species. An arbitrary threshold of 75% of footprint sets along a trail was used to classify a species as a "trail walker". All species with less than 75% of the footprint sets following trails were classified as "off-trail walkers".

## *Sign survey data in relation to camera trap data*

Pearson correlations were calculated between the number of sets of footprints and the capture rates of each species per survey for all five surveys combined. The data was log10 transformed to approximate a normal distribution. The stronger the correlation, the more the two methods agree in their estimates of traffic along a trail. Correlations were calculated using different combinations of subsets of data. Three subsets for species: 1. trail walkers, 2 off-trail walkers and 3 all species. Three subsets for footprints: 1. following trails, 2 crossing trails, 3 all footprints. It was expected that the correlations between sign and camera data would be higher for species that used trails frequently than for species that do not use trails frequently and higher for tracks that follow trails rather than cross trails.

The correlations were also calculated for each separate survey since they differed in suitability for footprint production. For two surveys cameras were located off-trail as well as on trail (Juan Branch and Mexican Branch). For both surveys correlations were calculated between the frequency of footprint sets and the camera captures for just the trail camera locations and again for all camera locations (including off-trail cameras).

The capture rate (per100days) was calculated per survey for each species as an index of relative abundance and compared between each of the five survey areas in relation to the terrain (highland or lowland) and known hunting pressure (presence or absence of poaching in the area). Data for the Wari-extension survey (wari ext.) were included in this analysis (see Chapter 4). This was the only concentrated camera trap survey for which no sign survey was conducted.

## *Activity patterns of prey species*

Activity patterns of prey species were calculated in the same way as for jaguar and puma, described in Chapter 6. Pearson correlations were calculated between the 24-hour activity patterns of jaguars and pumas and the activity patterns of each prey species to measure the level of overlap in activity between the jaguars, pumas and the prey species. Frequencies were arc-sin transformed prior to analysis.

### *White-lipped peccaries, a special case*

The hypotheses were tested that jaguar and puma captures are higher when WL peccary are present. Presence of WL peccaries was defined as a 5-day period before and after a single capture of a WL peccary at a particular camera location. Paired *t*-tests were used to compare capture rate of jaguars and of pumas (captures per 100 days) between periods when WL peccary were present and periods when WL peccary were absent per camera. It was expected that both cats would be attracted to WL peccaries and so have an increased capture rate when they were present. The capture rates were log10 transformed to approximate a normal distribution.

The hypotheses that jaguars and pumas are attracted to WL peccaries were tested by comparing the frequency distribution of time intervals between consecutive captures of jaguars or pumas and WL peccary captures with a Poisson distribution of the same mean (using a $\chi^2$ test of association). A distribution that is more regular than Poisson random distribution would indicate avoidance between large cats and WL peccary, a more clumped than random distribution would indicate attraction between large cats and WL peccary.

## Results

Capture rates of prey species associated only weakly with habitat variables (Table 7.2). Pacas and tapirs were positively associated with water, especially the larger river systems for paca. All correlations with trail width were negative, suggesting that prey species avoided larger trails, though this was only significant for brocket deer. Tapirs and pacas were positively associated with the seasonality and age of trail indicating that these species preferred the freshly cut trails and avoided the established trail system. The correlations between capture rate of prey species and capture rate of both jaguars and pumas were low, and mostly negative and none significant for larger prey species suggesting that prey avoided trails used by cats. Both altitude and slope showed little relation with capture rate of prey species, probably due to the lack of variation in these variables in the area, providing little opportunity to explore these variables in more detail.

The stepwise regression had a low explanatory power of habitat variables for capture rate of prey species. The only two species having $r^2$ adjusted values > 0.10

were the tapir ($r^2 = 0.16$ for the variables distance from rivers and streams, $N = 119$) and the brocket deer ($r^2 = 0.11$ for the variable width of trail, $N = 119$).

Table 7.2 Spearman correlation matrix between the habitat variables, capture rates of jaguar and puma and the capture rate of prey species per camera. Significant correlations ($p < 0.05$) are in bold. $N = 119$ camera locations.

| | Armadillo | Brocket deer | Collared peccary | Currassow | Opossum | Paca | Tapir | White lipped peccary |
|---|---|---|---|---|---|---|---|---|
| Age of Trail | 0.12 | 0.09 | -0.08 | -0.13 | -0.12 | **0.24** | **0.24** | 0.01 |
| Seas. of Trail | 0.13 | 0.14 | -0.08 | -0.08 | -0.09 | 0.12 | **0.28** | 0.11 |
| Width Trail | -0.06 | **-0.28** | 0.11 | -0.14 | -0.09 | -0.20 | -0.12 | -0.09 |
| Altitude | 0.04 | 0.16 | -0.09 | **0.24** | 0.10 | 0.05 | -0.09 | 0.06 |
| Dist. River | -0.14 | -0.11 | -0.03 | -0.04 | 0.03 | **-0.34** | -0.17 | 0.06 |
| Dist. Stream | -0.04 | -0.06 | 0.05 | 0.08 | -0.06 | -0.07 | **-0.28** | -0.08 |
| Dist. Water | -0.06 | -0.01 | -0.03 | 0.00 | -0.43 | -0.10 | **-0.42** | -0.04 |
| Slope | 0.00 | 0.06 | -0.06 | 0.03 | **0.20** | -0.08 | 0.01 | -0.05 |
| Jaguar cap/100 days | -0.03 | **-0.26** | 0.07 | 0.00 | **0.22** | 0.08 | -0.15 | -0.03 |
| Puma cap/100 days | -0.08 | -0.18 | 0.02 | **0.18** | 0.09 | -0.15 | -0.01 | 0.07 |

## *Use of trails by prey animals*

The average trail width on which prey species were photographed was narrower than for jaguars and pumas (Table 7.3) The sample sizes of armadillo, collared peccary and opossum were low compared to the other species, indicating either that they live at low densities or that the cameras were not well placed to capture these species. Trail width was not correlated with maximum body weight (Appendix C) because the heaviest species (tapirs) frequently walked on relatively narrow trails (Pearson correlation, $r = 0.01$, $p = 0.97$, $N = 10$ for log10 transformed data). Exclusion of this outlier gave a positive correlation close to significance, suggesting that larger animals walk on larger trails ($r = 0.64$, $p = 0.07$, $N = 9$ for log10 transformed data).

The percentage of captures of tapir, paca, brocket deer and armadillo on river banks were higher than the other prey species (Table 7.3). The percentage of captures on river banks was the same for both jaguars and pumas, both lower than every prey species.

Table 7.3 Mean trail width (with standard deviation) where prey species and jaguars and pumas were captured and the percentage of captures on stream/river banks, ordered by mean width of trail.

| **Species** | **Trail width m (St. Dev.)** | ***N* captures** | **Water edge %** |
|---|---|---|---|
| **Brocket** | 105.3 ( 75.4) | 167 | 40 |
| **Paca** | 113.4 ( 98.2) | 140 | 35 |
| **Currassow** | 120.6 ( 63.8) | 181 | 22 |
| **Opossum** | 125.8 ( 79.8) | 57 | 7 |
| **Tapir** | 129.3 ( 66.2) | 128 | 38 |
| **WL peccary** | 132.5 ( 73.5) | 129 | 8 |
| **Armadillo** | 133.5 ( 67.9) | 52 | 35 |
| **C peccary** | 159.3 ( 76.0) | 51 | 14 |
| **Jaguar** | 176.4 (118.3) | 697 | 4 |
| **Puma** | 179.4 ( 96.0) | 607 | 4 |

Most of the smaller prey species crossed trails rather than followed trails (paca, armadillo and agouti, Table 7.4). Margays were an exception, which mainly followed trails as did the other cats species. Of the larger species, collared peccaries walked trails the least (60%), which could explain their low capture rate on cameras throughout the study. Even though brocket deer had a majority of tracks following the trail (71%), a large number of these tracks were found on the narrow trails of Mexican Branch and 6K line survey. A high percentage (83%) of WL peccary tracks followed trails. Most were of large groups inundating the trails with tracks suggesting that the herds tend to follow the trails and occasionally move off trail. Jaguar and puma tracks only followed trails and never crossed them. This confirms the extensive use of trails by the two large cats.

Table 7.4 Frequency of footprint sets (*N*) for each species (5 surveys combined) and the percentage of the footprints that followed the trail, ordered by percentage of following trail. Arbitrary threshold of 75% footprints following trails distinguished "on-trail walkers" from "off-trail walkers".

| **Trail use** | **Species** | **% footprint sets that follow trail** | ***N*** |
|---|---|---|---|
| **Off trail** | **Paca** | 31 | 13 |
| | **Armadillo** | 43 | 14 |
| | **Opossum** | 50 | 2 |
| | **Agouti** | 50 | 6 |
| | **C peccary** | 60 | 5 |
| | **Brocket** | 71 | 24 |
| **On trail** | **WL peccary** | 83 | 30 |
| | **Ocelot** | 92 | 25 |
| | **Coati** | 100 | 2 |
| | **Margay** | 100 | 6 |
| | **Tapir** | 100 | 34 |
| | **Jaguar** | 100 | 43 |
| | **Puma** | 100 | 64 |

Capture rates and number of footprint sets were weakly correlated ($\leq 0.56$) suggesting that the two indices of abundance are not interchangeable. The number of footprint sets of trail walkers following trails was significantly positively correlated with capture rate. This was not true for off trail walkers.

Table 7.5 Pearson correlations between the log10 total captures per species and log10 footprint sets per species combined for all surveys. Significant correlations ($p < 0.05$) are shown in bold.

| **Captures of species included in the analysis (based on Table 7.5):** | ***N*** | **Footprints included in the analysis:** Following trails | Crossing trails | All footprints |
|---|---|---|---|---|
| **Trailwalkers (>75%)** | **32** | **0.55** | 0.35 | **0.56** |
| **Off trail walkers (<75%)** | **20** | -0.06 | 0.12 | -0.14 |
| **All species** | **52** | 0.53 | 0.20 | **0.51** |

Sample sizes were high enough to allow calculation of the Pearson correlation between capture rate and number of footprints in four separate surveys (Table 7.6). The survey specific correlations were stronger than those of the combined data (Table 7.5). This suggests that the relationship between footprints and captures was trail specific, probably due to the variation in substrate between trails. Capture rates and number of sets of footprints crossing trails were not positively correlated in any of the surveys. No positive correlations were found for any of the data from the Antelope trail, probably because of low camera density. Both the Juan Branch and Mexican Branch survey trails had suitable substrates for footprints, and both surveys had cameras on and off-trail. The Juan Branch correlations remained significant ($p < 0.05$) and high when the off-trail camera data were included in the analysis. The Mexican Branch correlations were significant but decreased to none significance ($p > 0.05$) when the off-trail camera data were included in the analysis. The freshly cut trail with high densities of cameras (6k line) indicated a high relation between footprints and camera captures.

Table 7.6 For each area, Pearson correlations between the log10 total captures per species and log10 footprint sets per species. Significant correlations ($p < 0.05$) are shown in bold.

| **Captures of species included in the analysis from cameras of:** | ***N*** | **Footprints included in the analysis:** | | |
|---|---|---|---|---|
| | | **Following trails** | **Crossing trails** | **All footprints** |
| Antelope trail | 9 | 0.35 | -0.36 | 0.29 |
| 6K line trail | 10 | 0.59 | 0.52 | **0.69** |
| Mexican Branch trail | 12 | **0.82** | -0.06 | **0.78** |
| Juan Branch trail | 13 | **0.86** | -0.42 | **0.83** |
| **Captures from off-trail cameras in the area included in analysis** | | | | |
| Mexican Branch area | 12 | 0.46 | 0.29 | 0.53 |
| Juan Branch area | 13 | **0.77** | -0.21 | **0.85** |

Capture rate of each species was highly variable between the surveys (Table 7.7). Capture rates on the Antelope survey cannot be reliably compared with the capture rates on the other surveys trails because the number of cameras on the Antelope trail was lower than for the other surveys. Since pacas are associated with water, the low capture rate of pacas on the Mitchell Creek trail, which was further from large rivers than the other trails, may reflect a true low density of pacas in this area.

The comparison between the lowland areas with no poaching (6K line, Wari ext. and Mexican) was valid since all three trails had high numbers of at least 16 cameras. Tapir and armadillo were captured at a similar rate between the three non-poached lowland areas, whilst capture rates of brocket deer, curassow, collared peccary and WL peccary varied between the three areas. Variation in the capture rate of WL peccary was expected due to their nomadic lifestyle. The variation in the capture rates of the other species is less easily explained and may not reflect true variation in relative abundance between the areas.

The Juan Branch area was susceptible to poaching. This could explain the relatively low capture rate of brocket deer, collared peccary and WL peccary, which are all game species, compared to the other lowland survey areas. Capture rates of tapir, not a game species, were similar between the poached and non poached lowland areas. However pacas are a prized game species yet their capture rate was up to three times higher in the poached area versus non poached areas. The comparison of the indices showed too many anomalies between areas to trust comparisons between species.

Table 7.7 Mean capture rate (per 100 days) for prey species in the 5 surveys. The survey areas are separated according to terrain and presence or absence of poaching.

| | Highland No poaching | | Lowland No poaching | | | Lowland Poaching |
|---|---|---|---|---|---|---|
| | **Antelope** | **Mitchell** | **Mexican** | **6K line** | **Wari ext.** | **Juan Br** |
| **Armadillo** | 0.71 | 0.31 | 0.59 | 0.80 | 0.78 | 0.42 |
| **Brocket** | 0.00 | 2.01 | 1.67 | 2.40 | 0.59 | 0.42 |
| **C peccary** | 0.71 | 0.46 | 0.10 | 0.23 | 1.17 | 0.00 |
| **Currassow** | 1.42 | 1.24 | 1.76 | 2.40 | 0.98 | 1.04 |
| **Paca** | 0.00 | 0.15 | 1.57 | 1.14 | 1.95 | 4.58 |
| **Tapir** | 0.00 | 4.02 | 1.37 | 0.92 | 1.17 | 1.25 |
| **WL peccary** | 0.00 | 3.72 | 0.78 | 1.26 | 0.39 | 0.00 |

## *Activity patterns of prey species*

Brocket deer and both peccary species had diurnal activity patterns, the converse of the activity pattern of the two large cats (Figure 7.1). The activity patterns of armadillos, pacas and tapirs overlapped with the nocturnal habits of the two large cats. Only the paca and the tapir had significant positive correlations with the activity patterns of the two cats. Although positive, the correlation for armadillos was not significant. Based on the activity patterns of the prey species armadillo, paca and tapir had a higher chance of being predated by jaguars and pumas.

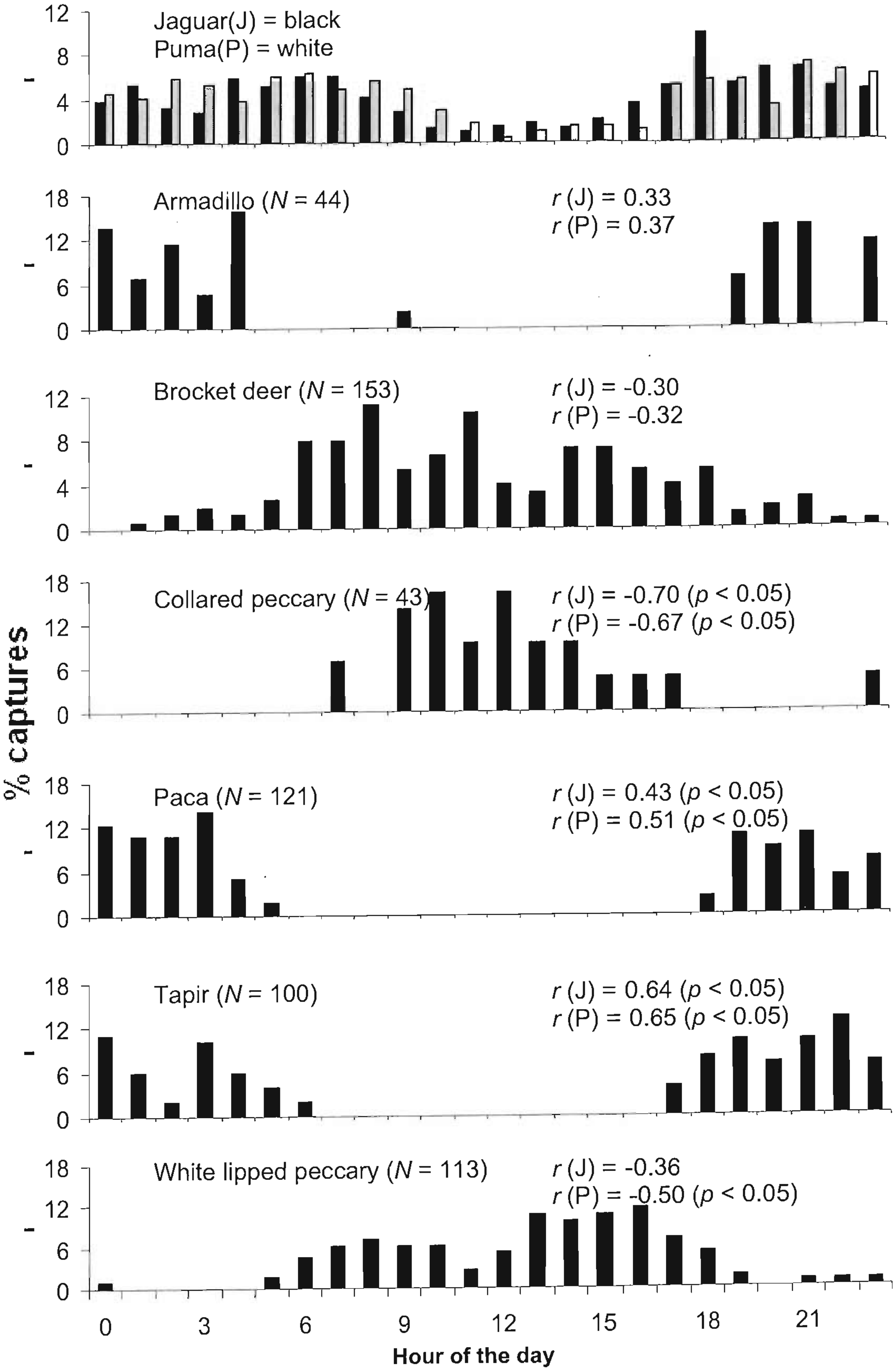

Figure 7.1 Activity patterns of jaguar, puma and prey species ($N$ = number of captures). Pearson correlations between activity pattern of prey and the two cats (jaguars = $r$(J) and puma = $r$(P), $N$ = 24) calculated per prey species.

### *Interaction of jaguars and pumas with white-lipped peccaries*

Jaguar capture rate was significantly lower when WL peccaries were present compared to when they were absent (mean capture rate 1.9 cap./100days and 2.9 cap./100 days respectively, paired $t = -2.72$, $N = 45$, $p < 0.01$, Appendix D: Table D.12). Jaguars therefore appear to avoid trails with WL peccaries, although they may follow them off-trail. Puma capture rate was non-significantly higher when WL peccary were present compared to when they were absent (mean capture rate 3.29 cap./100 days and 2.73 cap./100days respectively, paired $t = 1.22$, $N = 45$, $p = 0.23$, Appendix D: Table D.13). This might indicate that jaguars avoid WL peccaries, at least on trails, and no evidence was found that pumas actively follow WL peccaries.

Time intervals between a WL peccary capture and a cat capture had non-random frequency distributions for both jaguars and pumas ($X^2 > 1000$, d.f. $= 30$, $p < 0.01$). Both cat species had a higher proportion of captures than expected at $\leq 5$ days before or after a WL peccary capture (Figure 7.2a and b). This implies that both species were attracted to WL peccary. The attraction was more pronounced for pumas which had twice as many captures as jaguars 0-5 days before or afer a WL peccary capture. The long tails of the frequency distributions are due to the number of cat captures exceeding the number of WL peccary captures.

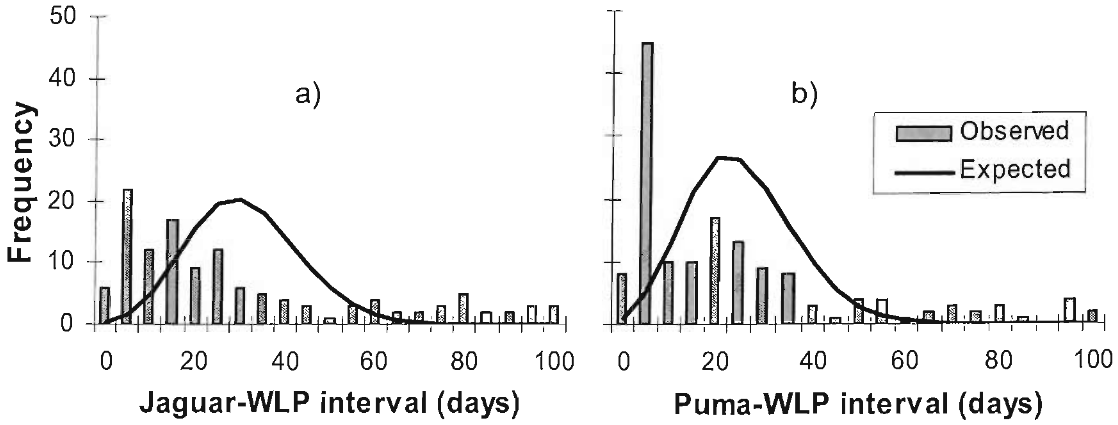

Figure 7.2 The frequency distribution of number of days between captures of a) jaguars and b) pumas and the closest capture of white-lipped Peccary (WLP) per camera location. The figure shows the data for the combined data of all the camera locations. The expected frequency was based on the Poisson distribution with a similar mean.

# Discussion

The camera trap data were used to compare differences in habitat use between potential prey species. These can be compared to habitat use of jaguars and pumas (see Chapter 4). There was little overlap between capture locations of prey species and large cats. Unlike jaguars and pumas, the prey species were generally found away from the larger trail systems. Paca and tapir captures were both associated with water. Previous studies have shown that pacas and tapirs frequent water systems (Beck-King et al. 1999, Tobler 2002). The agreement of the present camera data with this helps to justify camera traps as a reliable method for studying habitat preferences. However, the correlations were not strong indicating that a larger sample size of camera locations is needed using stratification of locations according to specific habitat variables.

Measuring abundance of prey species of large carnivores in the neotropics is extremely difficult. Relative abundance tends to be measured using sign surveys with intraspecific comparison between different locations (Granjon et al. 1996, Peres 1996, Escamilla et al. 2000, Cullen et al. 2001, Reyna-Hurtado & Tanner 2005). This study has shown that camera trapping along trails cannot immediately replace existing methods of sign surveys and distance sampling, as was assumed by Weckel et al. (2006). In similar manner as sign surveys, camera trapping should be useful as a relative abundance measure within species. The present study showed that the variation in the degree to which different species walked along trails and the variation in prey capture rates between relatively similar areas suggests that comparisons between trail-based camera trap data of different prey species are not reliable and even within species comparison might be problematic. The variation in capture rates of the same species between similar survey areas could be due to the variation in camera densities used. However, even the surveys in similar areas with a high density of cameras showed variation in the capture rates of some of the major prey species. This means that sign surveys in the neotropics are probably still the most reliable method for comparing within species abundance between different areas. Camera trapping could be used as an abundance measure if the relative trail use is known precisely for each species, such that absolute or relative abundance could be calculated with the use of capture rates and correction factors. This would require detailed study of capture rates per prey species across several different forest types and trail widths. These correction factors could be site specific which means that detailed study is necessary at each site before estimation of prey abundance.

Freshly cut trails were preferred by prey species over established trails. However the low sample size (2) was not sufficient to show whether newly cut trails are more or less, useful then established trails for estimating local abundance from captures. Between species comparison using camera traps will require high camera density grids that cover a wide area. The grids should include a range of different funnels (varying in width of trail and thickness of vegetation). The camera locations should be equally distributed between the different funnel types. Future camera trap study of prey species should focus on large grids of freshly cut trails with high densities of cameras. Weckel et al. (2006) analysed differences in capture rate within the Belizean rainforest along different types of trails, without reference to openness or width of trails or camera density, nor did they use a specific stratified design for the relative prey abundance index to allow unbiased comparison between species. As such, it can be assumed that the overall abundance indices reported by Weckel et al. (2006) were biased towards species most associated the trail type with the highest camera trap density.

Distributing cameras equally between different funnel types is logistically difficult. Furthermore, there is variation in habitat preferences between the species. Consequently any study aiming to compare abundance between species will require a single-species approach to estimate absolute abundance. This will avoid biases in the survey method which may favour one species over another. Future research should focus on a limited group of important prey species in an area and apply methods suitable for each particular species. For example, the use of burrow count surveys for pacas (Beck-King et al. 1999). The role of camera traps for estimating abundance of prey species should be reconsidered and evaluated per prey species.

Camera traps can be used for comparisons within species or for answering specific ecological questions concerning spatial and temporal distribution of species in relation to each other. The derivation of activity patterns from camera trapping is assumed to be unbiased and comparison between species legitimate. The present study has shown that the activity patterns of the potential prey species of jaguars and pumas varied considerably. The activity pattern of each species could influence its attractiveness to jaguars and pumas. For example certain species may be easier to overpower when they are resting, others may be easier to locate when they are active.

Only the activity patterns of tapir, armadillos and pacas were nocturnal and similar to jaguar and puma activity patterns. All other species were mainly diurnal. The relationships between prey activity patterns and the diet of both large cats, derived from scat data, are explored in Chapter 8.

This study showed that camera traps can be successfully used to detect localised presence of WL peccaries. Using camera traps in this way requires that the capture probability is high enough to reliably detect when the target species is present or absent. This does seem to be true for WL peccary in this study due to their high trail use. WL peccaries are suited for capture on cameras set for jaguars and pumas and many photos were taken when herds passed a camera location. When WL peccaries were present, no evidence was found for a change in puma capture rate but jaguar capture rate was significantly lower. This rejects the hypothesis that jaguars actively hunt for WL peccaries more than pumas. This finding was surprising, given the difference in body shape and size between the two cat species it was expected that jaguars would be more likely to tackle WL peccaries than would pumas. One alternative explanation could be that jaguars ambush WL peccaries and thus stay off trails to remain in cover. The diet data can be used to test this hypothesis by comparing the proportion of WL peccaries in the diet of both pumas and jaguars (Chapter 8).

# Chapter 8

# Diet of large felids in the Cockscomb Basin, Belize

## Abstract

The diet of jaguars and pumas varies across their geographic range within and between species. Jaguars and pumas living in open habitats have greater dietary overlap than those inhabiting dense jungle areas where jaguars tend to take larger prey species than do pumas.

Diet of jaguars and pumas inhabiting the CBWS in Belize was analysed using scats collected from different areas of the CBWS over 3 years. Diet varied considerably between different areas and between years. Short-term diet studies based on scats collected from smaller areas should be treated as temporary and localised descriptions of diet in an area.

No relation was found between scats found on trails and the availability of prey along the trails indicating that the cats mainly hunt off trail.

## Introduction

Availability of food is the most limiting factor for the survival of large felids, for example the greatest threat to tiger survival is the reduction in prey abundance (Karanth & Stith 1999). If the dietary requirements of the target species are understood then prey availability can be used to predict survival. If multiple carnivore species compete for the same prey resource then the influence of interspecific competition on survival of the target species needs to be understood and incorporated into the model. The aim of this chapter is to study the diet of two sympatric cats, the jaguar and the puma, in the CBWS, in Belize where both species are abundant (Chapter 6), using one of the largest and longest running scat collections for both species.

The relationship between prey availability and carnivore survival is relatively simple if the carnivore specialises on a single prey species, for example Canadian lynx (*Lynx canadensis*) predate exclusively on snowshoe hare (*Lepus americanus*, Mills et al. 2005) and black footed ferrets (*Mustela nigripes*) predate exclusively on prairie dogs (*Cynomys sp.*, Vargas 1996). Often the relationship is more complicated; many large carnivore species utilise a wide variety of prey species and switch prey according to availability, for example lions (Hayward & Kerley 2005), tigers

(Sunquist et al. 1999), wolves (*Canis lupus*, Ginsberg & Macdonald 1999), hyaenas (Henschel & Skinner 1990), leopards (Hayward et al. 2006) and dholes (Ginsberg & Macdonald 1999). Carnivores may switch between maximizing energy intake (selective hunting) to a strategy of hunting according to availability and vulnerability (opportunistically, Griffith 1975). To understand the effect that a reduction in prey abundance would have on the survival of a generalist carnivore, it is necessary to know the preferred prey and the cost of switching prey.

The presence of other sympatric generalist carnivore species will further complicate the relationship between prey availability and survival. Some generalist carnivores coexist by resource partitioning based on size of prey, facilitated by size differences between the carnivore species, for example resource partitioning between tigers, leopards and dholes in Nagarahole in India (Karanth & Sunquist 1995; Karanth & Sunquist 2000). The mechanism of co-existence of similar sized sympatric carnivores is less clear. Jaguars and pumas are similar sized (Chapter 1). Both species are able to take every species of potential prey within their ranges (Chapter 7) and both species use similar habitat and have similar activity patterns (Chapter 6). It is therefore hypothesised in this chapter that coexistence between the two species is facilitated by differences in prey selection.

It has been suggested that pumas eat smaller prey in areas where they coexist with jaguars (Iriate et al. 1990). Aranda & Cordero (1996) suggested that jaguars specialise on peccary and pumas specialise on deer. Several studies from different regions have described the diets of sympatric jaguar and puma populations (Rabinowitz & Nottingham 1986, Emmons 1987, Taber et al. 1997, Núñez et al. 2000, Scognamillo 2003, Crawshaw & Quigley 2002, Leite & Galvão 2002, Oliviera 2002, Novack et al. 2005). Habitat variation in dietary overlap and in prey type or size is examined in this chapter by comparing these studies and the current study of jaguar and puma diet.

Jaguar and puma scats cannot be distinguished reliably in the field. Emmons (1987) suggested that scats from the two species differ in diameter but this has been refuted by genetic evidence (Farrell et al. 2000). Some studies have assigned species based on footprints around the scat (Rabinowitz &Nottingham 1986, Núñez et al. 2000). In this study insufficient signs were found around scats to assign species. Bile acid analysis has been used to differentiate scats between jaguars and pumas but was only 80% accurate (Taber et al. 1997). Genetic analysis can type jaguar and puma scats with 100% accuracy (Farell et al. 2000); however this method is costly and labour intensive, and the genetic material degrades with the age of the scat and the field conditions (for example heavy rain and intense sunlight). Consequently many scats within a sample will not be suitable for genetic analysis and the success rate of typing scats successfully is ~25% (pers. comm. G. Amato, director of genetic research, Wildlife Conservation Society).

This study attempts to use dogs to distinguish between jaguar and puma scats on the basis of scent alone. The efficiency of finding scats by a single dog team, one trained dog and one handler, can be up to 400% that of people (pers. comm. B. Davenport, Director of Packleaderdog). Dogs have been used successfully to separate scats of grizzly bear (*Ursus arctos*) and black bear (*Ursus americanus*, Wasser et al. 2004) and swift foxes (*Vulpus felox*), red foxes and coyotes (*Canis latrans*, Smith et al. 2003). This is the first time that this method has been used for tropical carnivores and if successful would greatly lower the cost and increase the efficiency of detecting and identifying scats of tropical carnivores. Bininda-Emonds et al. (2001) created the phylogeny of larger cats based on olfactory chemicals found in faecal material. Jaguars and pumas differed substantially, with jaguars being placed in the *Panthera* genus and pumas in a separate group with cheetahs. This finding strengthens the hypothesis that dogs can differentiate between olfactory cues in jaguar and puma scats. The results of this study are not yet available due to unforeseen delays, but the method will nevertheless be discussed.

The CBWS has been a protected against hunting and extraction for 20 years. Diet of the two cats is compared with the findings of Rabinowitz & Nottingham (1986) who conducted diet analysis in the area during the 1980s when it was heavily logged and supported a community of hunters. Differences in diet between now and 1986 provide an indirect measure of the effect that protection of the area has had on the prey assemblage.

Novack et al. (2005) showed that the diet of jaguars and pumas in Guatemala was not influenced by human hunting, even though hunted areas had lower abundance of large prey species. In this current study the diet of cats inhabiting the edge of the CBWS where there is high poaching pressure, was compared with the diet of cats inhabiting the interior, where there is negligible poaching pressure, to determine whether the two cat species differ in their prey choice when the availability of certain species is reduced.

Diet studies are often based on the collection of scats during short-term surveys from localised areas (e.g. a specific trail where scat encounter rate may be high). They rarely consider the length of time over which the scats were collected or whether the sampling sites adequately represent the study area. Such diet studies may be biased by the sampling location and/or the sampling period. This study tests whether cat diet varied between four different sites within the study area from year to year over a 3-year period.

Diet analysis can provide information on food preferences only if it is combined with information on prey availability or abundance. In this study prey abundance could not be estimated from the camera trap and sign survey data without bias (Chapter 7). Two studies discuss the availability of prey in relation to jaguar diet: in Belize (Rabinowitz & Nottingham 1986) and in Manu, Peru (Emmons 1987). Both described a similar pattern in which jaguars took prey species according to their availability. Armadillos were most frequently eaten and the most abundant prey species in the Belizean study. In Peru a wide variety of prey was taken according to availability and dominated by river turtles.

Two further studies discuss the availability of prey in relation to both jaguar and puma diets. Scognamillo et al. (2003) found that jaguars in the Venezuelan Llanos preferred to eat larger prey animals irrespective of availability. More capybara and collared peccaries (*Tayassu tajacu*) were taken than expected according to their availability; white-lipped peccaries (*Dicotyles pecari*) were taken in proportion to their availability and white-tailed deer (*Odocioleus virginianus*) were taken at lower levels than available. All the smaller species were taken below availability. Pumas selected for all larger species according to their availability. Novack et al. (2005) found a difference between jaguars and pumas in the frequency of prey taken in the Peten, Guatemala. Jaguars specialised on coatis and armadillos, whilst pumas focused on brocket deer.

Pumas use trails significantly more often than jaguars (Chapter 6). Jaguars have a stocky build and so are well adapted to moving through a dense forest environment whilst pumas are long-limbed so more suited to open areas. It is therefore suggested that jaguars are not limited to trails in their hunting; instead they use trails as travelling routes and also hunt off-trail, whilst pumas use trails both for travelling and hunting. It was hypothesised that if jaguars and pumas hunt opportunistically then the overlap between prey availability on trails and diet is larger for pumas than for jaguars. We used camera trap data to estimate prey availability along trails, and this was compared with prey composition of scats found along the same trails. Camera traps give unbiased estimates of prey availability along trails and they should not be confused with potential bias for estimating prey abundance in an area.

The objectives of this chapter are:

1) To compare dietary overlap of jaguar and puma across their range by comparing results of different diet studies.

2) To test a new method for distinguishing between scats of jaguars and pumas by comparing the use of dogs with genetic analysis.

3) To compare diet of jaguars and pumas based on scats between different sites within CBWS and between different years.

4) To test whether jaguars and pumas take prey according to availability along trails within the CBWS.

# Methods

## Habitat variation in dietary overlap of jaguars and pumas

The percentage occurrences of different prey species in the diet were compared between and within 8 sets of data from studies across jaguar and puma geographic range (Mexico, Belize, Guatemala, Paraguay, Venezuela, Peru and Brazil). Although the CBWS dataset could not yet be added to these results for comparison, the results were presented to show trends of differences between jaguar and puma diet. Four of the studies were conducted in dense forest habitat and four in relatively open habitat. The level of niche overlap (Pianka index, Krebs 1994) between jaguars and puma diet was calculated for 7 of the datasets (the scat sample size was too low to do this for one dataset).

## Use of dogs to distinguish between jaguar and puma scats

To investigate dietary differences between jaguars and pumas in the CBWS, 445 scats were collected opportunistically over 3 years, across a ~200km$^2$ area. Scats of known origin, jaguars and pumas, were collected from the Belize Zoo and private owners, to train the dogs on the specific scent of jaguars and pumas. Scats were collected from eight jaguars, four males and four females, and seven pumas, four males and three females. The diets of captive cats were varied to ensure that the dogs were not trained to focus on a diet related odour rather than species specific odours. The age of the training scats was varied to imitate the age variation of scats found in the field. Two dogs were trained on each cat species to enable within and between species validation: the scat selection by the two dogs trained on the same cat species should show high levels of overlap, while the scat selection of the two pairs of dogs, each pair trained to select different cat species, should show low overlap. In addition 35 scats of known jaguar and puma origin, unknown to the dog trainers, were added to the field samples. As an additional validation a random sample of 40 scats were genetically analysed and compared with the results of the dogs.

## Scat Analysis

Many carnivores ingest prey whole, including hair and bones. A reference collection of hairs and bones from potential prey species in the area was used to identify hairs in scats. The reference material for this study was collected from road kill animals, captive animals at the Belize Zoo or donated by local hunters. Macroscopically the hairs differ in colour, pattern, length, width and texture. Microscopically, the medulla width and pattern and the scale pattern of cells may differ. Scale pattern was observed by making imprints of the hairs in gelatine. Bones were measured to draw inferences about the size of the animal. Teeth and claws are distinct for many species. Valdes (2006) used this material to create a reference key to identify the contents of scats to species level.

Locations of the scats are shown in Figure 8.1. Scats were also collected in the neighbouring Bladen Nature Reserve but they were of unknown location since the information was not recorded precisely by field staff.

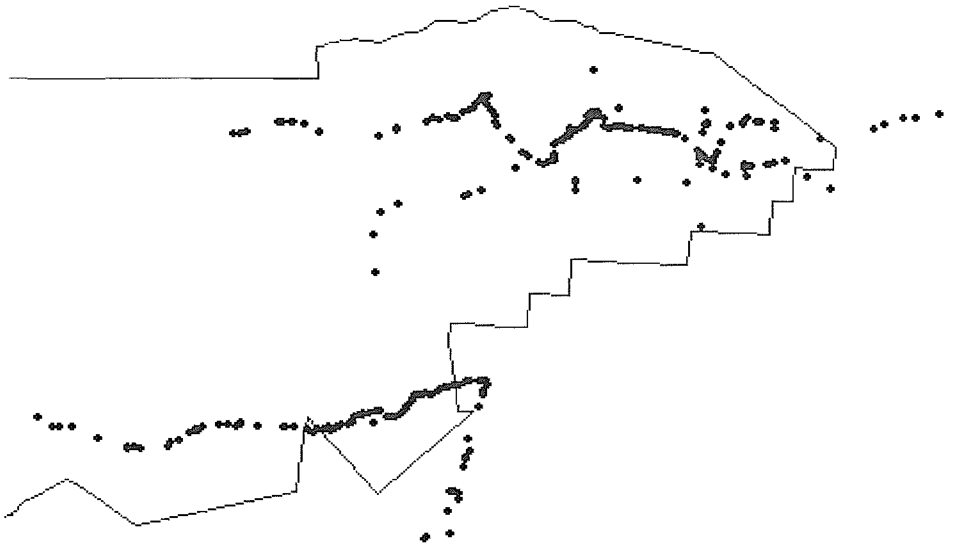

Figure 8.1 Locations of the 426 scats in and around the CBWS.

Each scat could contain multiple prey items (i.e. more than one species). The percentage occurrence of prey was calculated per prey species as: {total number of prey items of species A, present in all scats/total number of prey items in all scats}x100. This measure is often used to compare diet between areas or species; however the number of scats produced depends on the size of the prey eaten. More scats are produced if the prey is larger, but relatively more waste material is produced if the prey is smaller because the surface area:volume (hair and skin:meat) is larger. To correct for this bias, the biomass consumed per scat was estimated using the correction factor of Ackerman et al. (1984):

Weight of food consumed per scat = 1.98+0.035 ×{mean live weight of prey species}

Biomass consumed gives an unbiased estimate of the actual biomass, in terms of prey weight, that each species contributed to the diet of the cats. The mean prey weight followed Novack et al. (2005) because the prey data from this study in Guatemala were regionally most comparable to the present study. Table 8.1, based on Novack et al. (2005) shows the mean weights of the prey species found in the scats and the estimated weight of food consumed per scat (based on Ackerman et al. 1984).

Table 8.1 Mean weight of prey species (based on Novack et al. 2005) and the estimated weight of food consumed per scat (based on Ackerman et al. 1984).

| Weight Class | Species Common name | Species Scientific name | Mean live Weight (kg) | Corrected weight/ per scat (kg) |
|---|---|---|---|---|
| >10kg | w.t.deer | *Odocioleus virginianus* | 35.3 | 3.21 |
| | w.l.peccary | *Dicotyles pecari* | 29.4 | 3.01 |
| | c.peccary | *Tayassu tajacu* | 17.5 | 2.59 |
| | brocket deer | *Mazama Americana* | 16.7 | 2.56 |
| 5-10kg | tamandua | *Tamandua mexicana* | 6.2 | 2.20 |
| | paca | *Agouti paca* | 6.0 | 2.19 |
| | raccoon | *Procyon lotor* | 5.6 | 2.18 |
| <5kg | armadillo | *Dasypus novemcinctus* | 4.7 | 2.14 |
| | kinkajou | *Potos flavus* | 3.3 | 2.10 |
| | coati | *Nasua nasua* | 3.2 | 2.09 |
| | agouti | *Dasyprocta spec.* | 2.8 | 2.08 |
| | grey fox | *Urocyon cinereoargenteus* | 2.7 | 2.07 |
| | grison | *Galictis vittata* | 2.4 | 2.06 |
| | porcupine | *Coenou mexicanus* | 2.0 | 2.05 |
| | opossum | *Didelphis marsupialis* | 1.5 | 2.03 |
| | g.f.e opossum | *Philander opossum* | 0.9 | 2.01 |

## *Temporal and spatial variation in diet within the CBWS*

The study area within the CBWS included four distinct trail systems, each of which supported different jaguars (Chapter 3). The topography and distance from villages, thus the accessibility to hunters, differed between the areas.

Locals hunt for game around the boundary, and sometimes within the CBWS. Favoured forest game species are white-lipped peccaries, collared peccaries, red brocket deer and pacas (pers. obs. B. J. Harmsen, thesis author). Armadillos are also hunted but not necessarily in the forest as they are also common around village milpas. It was hypothesised that diet of the cats would differ between areas with high and low human hunting pressure. Diet was compared between the lowland forest in the interior of the CBWS where there is negligible hunting pressure, the lowland forest at the edge of the CBWS where there is high hunting pressure (frequent signs of hunters are encountered since it is accessible on foot from the nearby villages) and the highland forest inside and at the edge of the CBWS (both less accessible to hunters).

Diet was compared between the years over 3 years for those areas with sufficient scat samples. Data from the entire study area were compared with the findings of Rabinowitz & Nottingham (1986) to determine whether diet has changed during the 20 years of lowered human hunting pressure following the establishment of the protected status of the CBWS.

### *Variation in diet with the availability of prey on trails*

Camera trap data of prey species are biased towards prey species that walk trails (Chapter 7) and thus are unsuitable for estimating overall prey abundance in the forest. They are suitable for the estimation of prey availability along trail systems. Scats were collected during systematic sign surveys along four established trails. Prey species were monitored along the same trails using camera traps. The availability of each prey species along each trail was calculated as:

Number of captures of prey species / Total number of trap days × 100

The hypothesis that pumas hunt on trails more than jaguars was tested by calculating, for each trail, the Pearson correlation between the availability of prey species and the percentage of each prey species found in the diet. Similarity between diet and the availability of prey on the trail is evidence that jaguars or pumas use the trails to hunt opportunistically.

## Results

### *Habitat variation in dietary overlap of jaguars and pumas*

Diet varied within species between areas and between species in the same area without a clear pattern (Table 8.2). Peccaries were eaten in higher proportions by jaguars than by pumas across most of their range except in the Chaco area in Paraguay where the reverse occurred. There was a high level of dietary overlap ( > 75%) between jaguars and pumas inhabiting open areas (dry forest of Jalisco in Mexico; the Paraguayan Chaco; the Venezuelan Llanos and the Brazilian Pantanal). Dietary overlap was much lower ( < 35%) in areas of dense jungle (Manu in Peru, the Mayan Biosphere Reserve in Guatemala and the Atlantic forest in Brazil). In Manu and in the Atlantic forest jaguars took larger prey species than did pumas. A relatively high percentage of the puma diet in these areas was made up of rodents smaller than capybaras. In the Mayan Biosphere Reserve in Guatemala pumas took mainly deer and paca whilst jaguars took more peccary, armadillo and coatis.

Table 8.2 Percentage of prey items in scats Percentage occurrences of prey species in scats or percentage of kill remains found for jaguars (J) and pumas (P) and the Pianka index of dietary overlap in 8 locations across their range (ordered from left to right). The species are ordered by decreasing weight. Data sources: a= Rabinowitz & Nottingham 1986, b = Leite & Galvão 2002, c = Emmons 1987, d = Novack et al. 2005, e = Scognamillo et al. 2003, f = Crawshaw & Quigley 2002, g = Taber et al. 1997, h = Núñez et al. 2000.

| | | **Rainforest habitat** | | | | | | | | **Seasonal open habitat** | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **weight kg** | **Species** | **CBWS Belize** | | **Atl. for. Brasil** | | **Manu Peru** | | **MBR Guat.** | | **Llanos Venez.** | | **Pant. Brasil** | | **Chaco Parag.** | | **Jalisco Mexico** | |
| | | **J** | **P** | **J** | **P** | **J** | **P** | **J** | **P** | **J** | **P** | **J** | **P** | **J** | **P** | **J** | **P** |
| >10kg | livestock | - | - | 32 | 6 | - | - | - | - | - | - | 49 | 46 | - | - | - | - |
| | tapir | - | - | - | - | - | - | - | - | - | - | 2 | - | - | - | - | - |
| | puma | - | - | - | - | - | - | - | - | - | - | 2 | - | - | - | - | - |
| | giantanteater | - | - | - | - | - | - | - | - | 10 | - | - | - | 2 | 3 | - | - |
| | capybara | - | - | 8 | - | 3 | - | - | - | 21 | 10 | 14 | 32 | - | - | - | - |
| | w.t deer | - | - | - | - | - | - | 5 | 12 | 5 | 10 | - | - | - | - | 41 | 37 |
| | peccary | 5 | - | 26 | 1 | 16 | - | 18 | 7 | 40 | 19 | 31 | - | 5 | 9 | 16 | 7 |
| | brocket deer | 7 | - | 24 | - | 5 | - | 3 | 19 | - | - | 2 | 14 | 24 | 12 | - | - |
| | rhea | - | - | - | - | - | - | - | - | - | - | - | 4 | 1 | 1 | - | - |
| | small felid | - | - | - | - | - | - | - | - | - | - | - | - | 1 | - | - | - |
| | paca | 9 | - | 5 | 1 | 5 | 25 | 5 | 18 | - | - | - | - | - | - | - | - |
| | caiman | - | - | - | - | 8 | - | - | - | 7 | 10 | - | - | - | - | - | - |
| **total %>10kg** | | 21 | 0 | 95 | 7 | 37 | 25 | 31 | 57 | 90 | 73 | 98 | 96 | 32 | 25 | 57 | 44 |
| 5-10kg | spider monkey | - | - | - | - | 3 | - | 3 | 9 | - | - | - | - | - | - | - | - |
| | tamandua | 9 | - | - | - | 3 | - | 1 | - | - | - | 2 | - | 2 | 2 | - | - |
| | raccoon | - | - | - | - | - | - | - | - | 5 | - | - | - | - | - | - | - |
| | armadillo | 54 | - | - | 23 | - | - | 34 | 2 | - | 2 | - | 4 | 8 | 11 | 14 | 9 |
| | coati | 1 | - | - | - | - | - | 22 | 1 | - | - | - | - | - | - | 17 | 4 |
| | iguana | 2 | - | - | 3 | - | - | - | - | - | - | - | - | - | - | 6 | 12 |
| | river turtle | 1 | - | - | - | 24 | - | - | - | - | - | - | - | 2 | - | - | - |
| | snake | 1 | - | 3 | 3 | - | 17 | - | - | - | - | - | - | 1 | - | - | 1 |
| | unk. Reptile | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| **total % 5-10kg** | | 68 | 0 | 3 | 30 | 29 | 17 | 60 | 12 | 5 | 2 | 2 | 4 | 12 | 13 | 38 | 27 |
| 1-5kg | kinkajou | 1 | - | - | - | - | - | 1 | 4 | - | - | - | - | - | - | - | - |
| | olingo | - | - | - | - | 3 | - | - | - | - | - | - | - | - | - | - | - |
| | sloth | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| | agouti | 4 | - | - | 8 | 8 | 33 | 6 | 20 | - | 2 | - | - | - | - | - | - |
| | cap. monkey | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| | grey fox | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| | skunk | 1 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| | porcupine | - | - | - | - | - | - | - | 1 | - | - | - | - | - | - | - | - |
| | opossum | 4 | 33 | - | - | 6 | - | - | - | - | - | - | - | 10 | 16 | 2 | 4 |
| | rabbit | - | - | - | 16 | - | - | - | - | 2 | 7 | - | - | 24 | 9 | - | - |
| | dus. t. monkey | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| | desert cavia | - | - | - | - | - | - | - | - | - | - | - | - | 6 | 5 | - | - |
| | bird | 1 | - | 3 | 17 | 11 | - | 2 | 6 | 2 | - | - | - | 2 | 6 | 3 | 2 |
| **total % 1-5kg** | | 10 | 33 | 3 | 41 | 27 | 33 | 9 | 31 | 4 | 9 | 0 | 0 | 42 | 36 | 5 | 6 |
| <1kg | small lizard | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 4 |
| | amphibians | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| | bats | - | - | - | 1 | - | 8 | - | - | - | - | - | - | - | - | - | - |
| | crustacea | - | - | - | 2 | - | - | - | - | - | - | - | - | - | - | - | - |
| | fish | - | - | - | 7 | 5 | - | - | - | - | - | - | - | - | - | - | - |
| | insects | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| | small rodents | 1 | 67 | - | 11 | - | 17 | - | - | - | 17 | - | - | 14 | 26 | - | 19 |
| | mollusks | - | - | - | 1 | 3 | - | - | - | - | - | - | - | - | - | - | - |
| **total % <1kg** | | 1 | 67 | 0 | 22 | 8 | 25 | 0 | 0 | 0 | 17 | 0 | 0 | 14 | 26 | 0 | 23 |
| | data used | scats | | scats | | scats | | scats | | scats | | kills | | scats | | scats | |
| | sample size | 185 | 3 | 32 | 131 | 25 | 7 | 76 | 145 | 42 | 42 | 59 | 31 | 135 | 120 | 50 | 65 |
| | Pianka index | | | 0.16 | | 0.23 | | 0.34 | | 0.73 | | 0.79 | | 0.80 | | 0.85 | |
| | source | a | | b | | c | | d | | e | | f | | g | | h | |

## Use of dogs to distinguish between jaguar and puma scats

The dog trials were not completed in time for this thesis. Consequently conclusions could be made about the diet of big cats, jaguar and puma combined, but not about differences between jaguar and puma diets in CBWS. In the following section it is assumed that scats of the two species were evenly distributed through the areas since jaguars and pumas were equally active in all areas (supported by evidence in Chapter 6).

## Temporal and spatial variation in diet within the CBWS

The mean number of prey species per scat was 1.12. One scat contained 3 species, 50 contained two species and 394 contained only 1 species. The percentage occurrences of prey species in the diet were calculated for: the entire study area within the CBWS, the four different areas within the CBWS (lowland edge, lowland interior, highland edge, highland interior) and the neighbouring bladen reserve (Table 8.3). A total of 16 species of mammal were found in the diet. Reptiles and birds were also identified but at low levels; the most frequent non-mammal species in the diet were iguanas (5.1% of scats) in the lowland interior area during the wet season of 2003.

Armadillo was the most common prey species in scats throughout the study area except in the lowland interior where pacas were more frequently eaten. Pacas were consistently found in high percentages in the diet in areas with adequate sample sizes. Larger prey species ( > 10 kg) made up 19.7% of the diet; of these white-lipped peccaries were most common and collared peccaries least common in the diet throughout the study areas. Kinkajous, (arboreal), and coatis (semi-arboreal) were found consistently in the diet but varied between the areas. Coatis prefer forest edge to the dense interior (Reid 1997). The relatively high percentage of coatis in the diet (12%) in the lowland forest at the edge of the CBWS was indicative of disturbed habitat. White-tailed deer are not present in the CBWS (Chapter 7) therefore the presence of white-tailed deer in scats found in the lowland forest at the edge of the CBWS indicates that the cats utilising this habitat also hunt in the savannah areas beyond the forest buffer of the CBWS. Similarly the presence of white-tailed deer in the scats from the Bladen area must be associated with the neighbouring open savannah area close to Bladen from which a large part of the scats were collected.

Table 8.3 Percentage occurrences of prey species in scats collected in the CBWS (lowland edge, lowland interior, highland edge, highland interior) and in the Bladen Nature reserve. Species are ordered by decreasing mean weight.

| **Weight Class** | **Species** | **Totals** | **Bladen** | **Low edge** | **Low interior** | **High edge** | **High interior** |
|---|---|---|---|---|---|---|---|
| >10kg | tapir | - | - | - | - | - | - |
| | w.t.deer | 0.4 | 5.3 | 0.9 | - | - | - |
| | w.l.peccary | 8.3 | 10.5 | 4.6 | 7.1 | 15.4 | 5.6 |
| | c.peccary | 4.7 | 5.3 | 1.9 | 5.1 | 6.4 | 5.6 |
| | brocket deer | 6.3 | 10.5 | 3.7 | 7.6 | 6.4 | 5.6 |
| | ocelot | - | - | - | - | - | - |
| **Total% >10kg** | | 19.7 | 31.6 | 11.1 | 19.8 | 28.2 | 16.7 |
| 5-10kg | river otter | - | - | - | - | - | - |
| | jaguarundi | - | - | - | - | - | - |
| | tamandua | 1.1 | 10.5 | - | 1.5 | - | - |
| | paca | 20.1 | - | 19.4 | 26.9 | 16.7 | - |
| | howler monkey | - | - | - | - | - | - |
| | raccoon | 0.4 | - | 1.9 | - | - | - |
| **Total % 5-10kg** | | 21.7 | 10.5 | 21.3 | 28.4 | 16.7 | 0.0 |
| <5kg | armadillo | 27.3 | 21.1 | 32.4 | 22.3 | 23.1 | 50.0 |
| | tayra | - | - | - | - | - | - |
| | margay | - | - | - | - | - | - |
| | kinkajou | 4.0 | 10.5 | 1.9 | 3.6 | 6.4 | 5.6 |
| | coati | 7.2 | 5.3 | 12.0 | 6.1 | 2.6 | 11.1 |
| | agouti | 1.6 | 5.3 | 1.9 | 1.0 | - | 5.6 |
| | skunk | - | - | - | - | - | - |
| | grey fox | 0.2 | - | - | 0.5 | - | - |
| | grison | 0.4 | - | - | - | 1.3 | 5.6 |
| | porcupine | 0.7 | 5.3 | 0.9 | 0.5 | - | - |
| | opossum | 2.0 | - | 1.9 | 3.0 | 1.3 | - |
| | g.f.e opossum | 0.4 | - | - | 1.0 | - | - |
| **Total % <5kg** | | 43.8 | 47.4 | 50.9 | 38.1 | 34.6 | 77.8 |
| Non-mammal | bird | 0.7 | - | 1.9 | 0.5 | - | - |
| | iguana | 2.2 | - | - | 5.1 | - | - |
| | lizard | 0.2 | - | - | - | 1.3 | - |
| | snake | 1.1 | - | 0.9 | 2.0 | - | - |
| **Total % non-mammal** | | 4.3 | 0.0 | 2.8 | 7.6 | 1.3 | 0.0 |
| **% unknown** | | 10.5 | 10.5 | 13.9 | 6.1 | 19.2 | 5.6 |
| ***N* prey items** | | 447 | 19 | 108 | 197 | 78 | 18 |

Over the entire study area, small species ( < 5 kg) contributed greater percentage biomass (48%) than medium or large sized prey (Figure 8.2). There was spatial variation in the percentage biomass contribution of different weight classes of prey to the diet in the different areas. The biomass contribution of the large and medium size prey species ( > 10 kg and 5-10 kg) was lower in the lowland area at the edge of CBWS where there was human hunting pressure compared to the interior lowland and highland areas where human hunting pressure was negligible. Small species ( < 5 kg) contributed to ~60% of the diet in this hunted area (Figure 8.2).

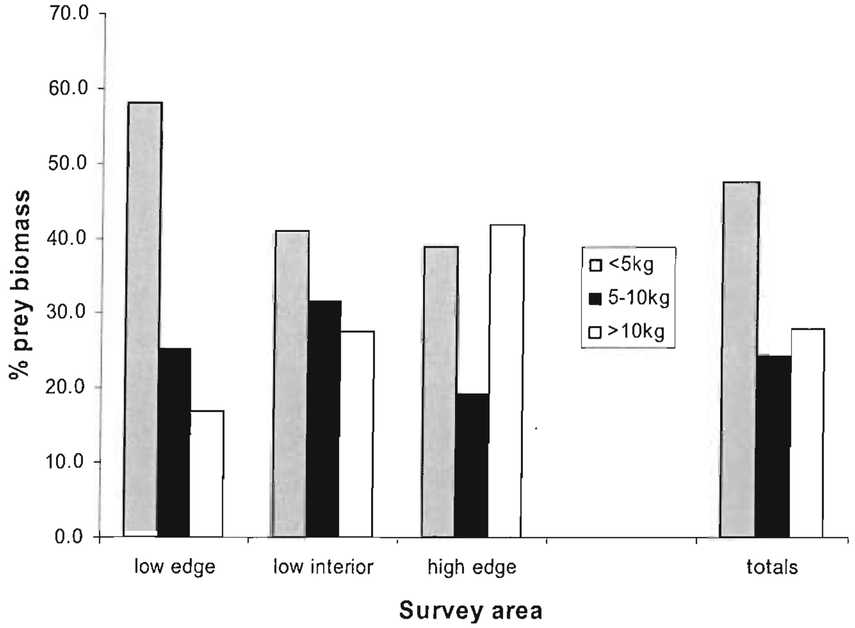

Figure 8.2 The percentage biomass contribution to cat diet, using correction factor of Ackerman et al. (1984), of the three weight classes of prey species at three separate sites within the CBWS with adequate sample size (*N* > 35).

The number and type of prey species taken in the diet varied between the years (Table 8.4; note that the sample sizes for some years or areas were low so care should be taken when interpreting the results). In the interior lowland area the percentage of armadillos in the diet increased from 2003 to 2005, whilst the percentage of large species ( > 10 kg) reduced by half between 2004 and 2005. Overall, a decrease in the biomass of large and medium species taken coincided with an increase in the biomass of small species ( < 5 kg) taken (Figure 8.3). This shift in diet also coincided with reports of hunting by poachers who entered the interior lowland of the CBWS by boat at the end of 2004.

Diet of cats in the lowland forest at the edge of CBWS (where there is hunting by humans) showed the least annual variation of the three areas. Pacas and armadillos were important in the diet every year (Table 8.4). In this area a decrease in the biomass of medium sized prey taken coincided with an increase in the biomass of small and large sized prey taken (Figure 8.3).

White-lipped peccaries were the only large species ( > 10 kg) to contribute to cat diet in the highland forest at the edge of the CBWS during 2003; in 2004 brocket deer and collared peccaries were also eaten (Table 8.4). In this area, armadillos were the most frequent prey item found in the diet (39%) during 2003 whilst pacas were not commonly eaten (4%); the reverse occurred during 2004 when paca were eaten most frequently (25%) and the occurrence of armadillo in the diet reduced (9%). Assuming that jaguars and pumas contributed similarly to the diet between years and areas, the data show a high plasticity in the diets of the two cats.

Table 8.4 Percentage occurrences of prey species in the scats collected in the three areas of CBWS in 2003, 2004 and 2005. The percentages are per trail system per year. Species are ordered by decreasing mean weight.

| **Weight class** | **species** | **Low edge** | | | **High edge** | | **Low interior** | | |
|---|---|---|---|---|---|---|---|---|---|
| | | **2003** | **2004** | **2005** | **2003** | **2004** | **2003** | **2004** | **2005** |
| | tapir | - | - | - | - | - | - | - | - |
| | w.t.deer | - | 2.3 | - | - | - | - | - | - |
| >10kg | w.l.peccary | 4.4 | 4.7 | - | 21.7 | 9.4 | 8.7 | 2.7 | 10 |
| | c.peccary | 4.4 | - | - | - | 12.5 | 5.6 | 5.4 | - |
| | brocket deer | 2.2 | 4.7 | - | - | 12.5 | 7.1 | 13.5 | - |
| | ocelot | - | - | - | - | - | - | - | - |
| **Total% >10kg** | | 11 | 11.7 | 0 | 21.7 | 34.4 | 21.4 | 21.6 | 10 |
| | river otter | - | - | - | - | - | - | - | - |
| | jaguarundi | - | - | - | - | - | - | - | - |
| | tamandua | - | - | - | - | - | 1.6 | 2.7 | - |
| 5-10kg | paca | 24.4 | 16.3 | 23.1 | 4.3 | 25 | 28.6 | 29.7 | 25 |
| | howler monkey | - | - | - | - | - | - | - | - |
| | raccoon | 4.4 | - | - | - | - | - | - | - |
| **Total % 5-10kg** | | 28.8 | 16.3 | 23.1 | 4.3 | 25 | 30.2 | 32.4 | 25 |
| | armadillo | 26.7 | 37.2 | 38.5 | 39.1 | 9.4 | 19.8 | 27 | 35 |
| | tayra | - | - | - | - | - | - | - | - |
| | margay | - | - | - | - | - | - | - | - |
| | kinkajou | 2.2 | - | 7.7 | - | 15.6 | 3.2 | 5.4 | 5 |
| | coati | 20 | 7 | - | - | 3.1 | 1.6 | 10.8 | 25 |
| <5kg | agouti | - | 2.3 | 7.7 | - | - | 0.8 | - | - |
| | skunk | - | - | - | - | - | 0.8 | - | - |
| | grey fox | - | - | - | - | - | - | - | - |
| | grison | - | - | - | - | - | - | - | - |
| | porcupine | 2.2 | - | - | - | - | 0.8 | - | - |
| | opossum | - | 2.3 | - | - | 3.1 | 2.4 | 2.7 | - |
| | g.f.e opossum | - | - | - | - | - | 0.8 | - | - |
| **Total % <5kg** | | 51.1 | 48.8 | 53.9 0 | 39.1 | 31.2 0 | 30.2 | 45.9 | 65 |
| | bird | - | - | 7.7 | - | - | 0.8 | - | - |
| Non-mammal | iguana | - | - | - | - | - | 7.9 | - | - |
| | lizard | - | - | - | - | 3.1 | - | - | - |
| | snake | 2.2 | - | - | - | - | 1.6 | - | - |
| **Total % non-mammal** | | 2.2 | 0 | 7.7 | 0 | 3.1 | 10.3 | 0 | 0 |
| **% unknown** | | 6.7 | 23.3 | 15.4 | 34.8 | 6.3 | 7.9 | 0 | 0 |
| ***N* prey items** | | 45 | 43 | 13 | 23 | 32 | 126 | 37 | 20 |

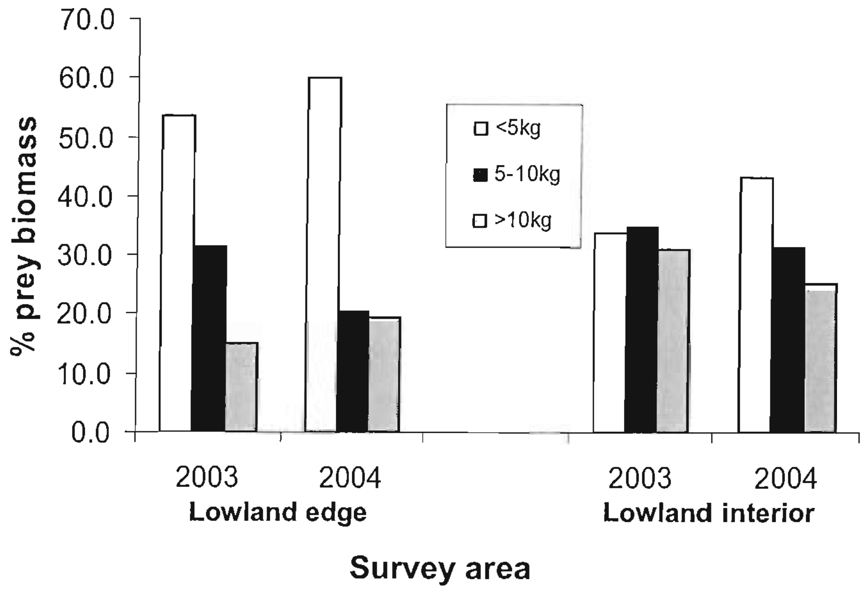

Figure 8.3 The biomass contribution, based on Ackerman et al. 1984, for the three weight classes of prey species for the years 2003 and 2004 for lowland edge areas and lowland interior areas.

The diet of big cats in CBWS appears to have altered since hunting by humans was prohibited in 1986 (Table 8.5). In 1984 cat diet in the area was dominated by armadillos (54%). Their contribution today has halved and the contribution of pacas to the diet doubled. Overall the frequency of small species ( < 5 kg) in the diet has decreased whilst the frequency of medium (5-10 kg) and large species ( > 10 kg) has increased, as might be expected if hunting were prohibited and game species were able to proliferate. The Pianka index between the study in the 1980's and the 2003 to 2005 diet was 0.85. This was lower than the mean Pianka index between the 3 years of the present study (0.93), indicating that there was a real change over the years.

It has to be noted that the 1980's data (Rabinowitz & Nottingham 1986) were jaguar diet and the present data were large cat diet. Only three scats of the 1980's study were attributed to puma and the remaining 185 to jaguars, based on signs around scats and telemetry data of five male jaguars. None of the scats were assigned unknown origin. This suggests that the method of assignment may have been biased towards jaguars, if so the 1980's data represent big cat diet as does the present study. Comparison between the two datasets is therefore valid.

Table 8.5 Comparison between percentage occurrence of prey in scat for the total dataset of scats for the present study and the study of Rabinowitz & Nottingham (1986). Species are ordered by decreasing mean weight.

| **Weight class** | **species** | **1983/4** | **2003/5** |
|---|---|---|---|
| | tapir | - | - |
| | w.t.deer | - | 0.4 |
| >10kg | w.l.peccary | 2.7 | 8.3 |
| | c.peccary | 2.7 | 4.7 |
| | brocket deer | 6.5 | 6.3 |
| | ocelot | - | - |
| **Total% >10kg** | | 11.9 | 19.7 |
| | river otter | - | - |
| | jaguarundi | - | - |
| | tamandua | 9.3 | 1.1 |
| 5-10kg | paca | 9.3 | 20.1 |
| | howler monkey | - | - |
| | raccoon | - | 0.4 |
| **Total % 5-10kg** | | 18.6 | 21.6 |
| | armadillo | 54.0 | 27.3 |
| | tayra | - | - |
| | margay | - | - |
| | kinkajou | 0.5 | 4.0 |
| | coati | 1.0 | 7.2 |
| <5kg | agouti | 4.3 | 1.6 |
| | skunk | 0.5 | - |
| | grey fox | - | 0.2 |
| | grison | - | 0.4 |
| | porcupine | - | 0.7 |
| | opossum | 3.2 | 2.0 |
| | g.f.e opossum | 1.0 | 0.4 |
| | small rodent | 1.0 | - |
| **Total % <5kg** | | 65.5 | 43.8 |
| | bird | 0.5 | 0.7 |
| Non-mammal | iguana | 1.5 | 2.2 |
| | lizard | - | 0.2 |
| | turtle | 1.0 | - |
| | snake | 0.5 | 1.1 |
| **Total % non-mammal** | | 3.5 | 4.3 |
| **% unknown** | | 0.5 | 10.5 |
| ***N* prey items** | | 185 | 447 |

## *Variation in diet with the availability of prey on trails*

There was a significant positive correlation between prey availability and cat diet along one of the four established trail systems (Pearson correlation $r = 0.67$, $p < 0.01$; Table 8.6). The other three trails yielded no such evidence of opportunistic hunting along trails. The cause of this difference between the trail systems is not clear. Overall few evidence was found for opportunistic hunting around trail systems.

Table 8.6 Pearson correlations between cat diet and prey availability along four different trail systems in the CBWS. Significant correlations in bold ($p < 0.05$).

| | **West 2003** | **West 2004** | **West 2005** | **West total** | **SSP 2004** | **SSP total** | **Vic total** | **Juan total** |
|---|---|---|---|---|---|---|---|---|
| Correlation | 0.46 | -0.03 | 0.07 | 0.29 | **0.67** | **0.49** | -0.09 | 0.12 |
| *N* scats | 126 | 37 | 20 | 183 | 32 | 64 | 18 | 108 |
| *N* photos | 56 | 27 | 24 | 106 | 15 | 47 | 40 | 19 |

## Discussion

Studies that were able to distinguish between jaguar and pumas scats showed wide variation in diet within and between species across their range. There was no evidence that jaguars are peccary specialists and pumas are deer specialists as was suggested by Aranda & Cordero (1996). In the four studies conducted in open habitats jaguars and puma diets overlapped by ~80%. In the three studies conducted in closed rainforest environments the similarity between jaguar and puma diets was much lower (~20%). In these dense areas of rainforest pumas ate smaller prey species than did jaguars. Iriate et al. (1990) suggested that pumas eat smaller prey species if they have to compete with jaguars. The closed rainforest environment has greater species richness than more open areas (Jenny 1996) but species' abundances are lower. As such there are more opportunities for diet partitioning in the rainforest, as there is more variation in potential prey, and this may be driven by competition for food since the overall prey biomass is relatively low. The open areas of the Brazilian Pantanal and the Venezuelan Llanos are characterised by a high abundance of relatively large wild and domestic prey species (Scognamillo et al. 2003, Polisar et al. 2003). High levels of persecution by local livestock farmers may keep the cat populations below carrying capacity such that competition is low or absent and both species can take the optimal prey.

The level of interspecific competition for prey between jaguars and pumas can only be properly understood if the relationship between diet of each cat and the prey availability is known. Success will be reflected in the higher density of either species.

It can be assumed that the higher the densities of one or both cat species the more optimal is the available prey assemblage. Long-term simultaneous study of all three variables in different habitats is necessary to understand the level of competition between jaguars and pumas. Comparison of abundance can only be used as a measure of competitive success when knowledge is available on the carrying capacity of each species in an area, in the absence of the other. These data are unattainable without a natural experiment of removing one of the species, which is unacceptable.

The majority of species in the diet of jaguars and pumas in the CBWS were small ( < 5 kg), predominantly armadillos, and medium-sized (5-10 kg), predominantly pacas. Large species ( > 10 kg) comprised ~20% of the diet, primarily white-lipped peccaries. The diet contained 16 different mammal species, which is similar to leopards, the only other similar sized cat species living in rainforest environment (Sunquist & Sunquist 2002, mean number prey species for leopards in rainforest environments = 14). In contrast tigers eat on average eight different prey species within an area, independent of the environment, including rainforest (Sunquist & Sunquist 2002). In areas where tigers and leopards live sympatrically, the leopard diet is wider than tiger diet (Sunquist & Sunquist 2002). The higher flexibility of leopard diet is one of the reasons that leopards can survive in areas from which tigers are disappearing. Jaguars and pumas show a similar level of plasticity in the diet as the leopard and therefore are more adaptable to survive in altering human dominated landscapes compared to inflexible species like tigers.

In contrast to Novack et al. (2005) cat diet differed between hunted and non-hunted areas. Before the Cockscomb Basin was protected in 1986 ~54% of the cat diet comprised armadillos. Today only ~27% of cat diet in the same area is of armadillos and the frequency of pacas in the diet has increased. It seems that human hunting pressure suppressed the paca population during the 1980s and that protection of the area may have facilitated their increase. Comparison between the frequency of armadillos and pacas in the diet of cats inhabiting the hunted area at the edge of the CBWS with those inhabiting the interior of the CBWS shows a similar pattern. These data are indirect evidence that paca abundance can fluctuate rapidly due to hunting pressure whilst armadillos may be a super-abundant prey which is taken in high numbers when larger prey are scarce.

Although the ungulate species (white-tailed deer, brocket deer, white-lipped peccary and collared peccary) made up a low proportion of the diet (~20%), there has been a 66% increase in the diet since the 1980's. Without data on ungulate abundance in the area it is not possible to determine whether this reflects low preference for ungulates in the diet or that the ungulate population is low and has not recovered since hunting declined after the land was protected in 1986.

White-lipped peccaries are a prized game species in Belize, earning up to $75 per individual. The effect of legal hunting of white-lipped peccaries outside the CBWS extends far into the protected area since the same herd may travel traverse the boundary. It is possible that herd size remains suppressed due to high hunting pressure at the edges of the CBWS. In Corcovado National Park in Costa Rica, where white-lipped peccaries are considered abundant, they contribute substantially to jaguar diet (~60%, pers. comm. E. Carrilo, jaguar researcher in Costa Rica, Wildlife Conservation Society). Collared peccaries have much smaller group home ranges than white-lipped peccaries (Keuroghlian et al. 2004, Judas & O'Henry 1999) therefore legal hunting of collared peccaries in the areas bordering the CBWS will have less impact on the collared peccary population within the CBWS. Pacas have small home ranges as well (Beck-King et al. 1999) and hunting of pacas in the areas bordering the CBWS will have little impact on the paca population within the CBWS. Further research on the relationship between the availability of large ungulates and their contribution to cat diet could enable scat analysis to be used as a rapid assessment of the health of prey populations in other areas.

Overall ~20 individual jaguars and an unknown number of pumas had the potential to contribute to the diet data. Each local area in this study supported a distinct set of jaguars, (~7 individuals per location) and an unknown number of pumas. Diet varied from year to year (over a 3-year period) and between the four different regions of the study area (~200 km$^2$). This indicates plasticity in the diet of either or both of the two cats; and that diet studies based the collection of scats during short-term surveys from localised areas may not be representative of the entire study area. In order to accurately estimate diet, long-term monitoring is necessary and the number of individuals that have the potential to contribute to the scat dataset should be taken into account.

The Ackerman et al. (1984) correction factor was originally used to calculate biomass consumed per scat by pumas. It is often because it is assumed that all large cats have similar digestive systems and that different prey species, not originally studied will have a similar correction factor (Karanth & Sunquist 1995, Núñez et al. 2000, Novack et al. 2005, Garla et al. 2001). This assumption has never been tested while variation can be expected between species of cat and between sizes of prey. The prolific use of this equation warrants validation with different cat species and different prey species.

The male bias found on camera traps along trails (Chapters 5 and 6) could reflect a male bias in scats. Many diet studies collect scats along established trails (Rabinowitz & Nottingham 1986, Emmons 1987, Taber et al. 1997, Núñez et al. 2000, Novack et al. 2005). A male biased presence on trails will result in a male biased scat sample. The sexual dimorphism of large felids, females are smaller than males, could influence diet selection. As such diet estimated from scats colleted from trails where males dominate may not reflect the population diet. Genetic analysis using markers for Y-chromosomes is planned to identify the sex of the scat producer. This will reveal the sex ratio in the present dataset and sexual differentiation in diet can be estimated if the sample sizes of male and female scats are high enough.

If the diet of a predator reflects prey availability then it can be assumed that hunting is opportunistic (there is no prey selection). In this study the diet of jaguars and pumas that walk on trails did not reflect the availability of prey species utilizing those trails. This does not mean that the two species are not opportunistic hunters, rather this question needs to be readdressed when the scats have been assigned as jaguar or puma. The greater use of trails by pumas compared to jaguars (Chapter 6) suggests that the diet of pumas will more closely reflect prey availability on trails than will the diet of jaguars. Testing this hypothesis will reveal whether either jaguars and/or pumas hunt opportunistically along trails.

## Future studies

Diet studies should be conducted with more structure beyond opportunistic scat collection. Repeat surveys to detect seasonal or annual fluctuations in diet should be considered. The number and sex of individuals contributing to the dataset should be estimated. If possible, systematic surveys should be conducted in combination with abundance estimates of both the predator species and the potential prey species. Once the relationship between diet, prey availability and densities of the competing predator species is understood, analysis of scats from under-studied areas of their range could be used as an indirect assessment of the both the health of the prey population and the viability of jaguar and puma populations.

# Chapter 9

# Marking behaviour of jaguars and pumas

## Abstract

In this study marking behaviours of jaguars and pumas were studied by comparing sign survey data with camera trap data along trails in the CBWS, Belize. The most commonly encountered marks were scrapes along the ground. Scrapes were spatially clustered along the trails indicating that individuals probably react to other scrapes by scraping in the same area. Scrape activity was more closely associated with puma captures than with jaguar captures. High scraping frequencies were not related to the presence of particular individuals, suggesting that scrape marking behaviour is not a sign of dominance in this area.

## Introduction

Marking behaviour in cats species includes spraying urine on vertical surfaces (Sanders 1963, Schaller 1967, Bailey 1974, Smith et al. 1989, Kitchener 1991), defecating (Smith et al. 1989, Rabinowitz & Nottingham 1986), scrapes on the ground (Seidensticker et al. 1973, Rabinowitz & Nottingham 1986, Smith et al. 1989), scratches on tree bark (Smith et al. 1989) and rubbing against objects (Smith et al. 1989). These behaviours have a territorial role (Smith et al. 1989, Kitchener 1991) and also function to attract mates when females are in oestrus (Smith et al. 1989, Kitchener 1991, Molteno et al. 1998). The aim of this chapter is to investigate the marking system of jaguars and pumas in the CBWS, Belize.

Often cats mark the boundary of their territory or home range. In Nepal where tigers held exclusive territories the contact zones between two individual male tigers had significantly more marking activity than the core areas (Smith et al. 1989). Changes in boundaries or the influx of new conspecifics were followed by an increase in marking activity. Individuals responded to marks of conspecifics by increasing marking in close proximity. Kitchener (1991) noted a similar ‘marking war’ on the boundaries of territories of Scottish wildcats (*Felis silvestris*). Female tigers increased their marking frequency to advertise to males that they were receptive (Smith et al. 1989). A similar increase in marking behaviour was found in female black-footed cats (*Felis nigripes*) in South Africa (Molteno et al. 1998).

There is not much literature about the communication of jaguars and pumas in the neotropics and that which exists is contradictory. Rabinowitz & Nottingham (1986) noted that jaguars in the Cockscomb Basin in Belize frequently scraped on the ground and often marked these scrapes with faeces whilst pumas rarely scraped in this area. In contrast Seidensticker et al. (1973) remark that scraping on the ground is the dominant method of marking by pumas in the United States. Scrape marks noted in Manu in Peru were assigned more often to pumas than to jaguars (Emmons 1987). In the Pantanal scrapes were rarely found and only in association with pumas (Schaller & Crawshaw 1980, Crawshaw & Quigley 1991). The function of scrape marking in jaguars and pumas is not clear between any of these studies.

Scrape marks on the ground were frequently encountered during the present study and were monitored by regular surveys along several transects. The lack of exclusive territories of male jaguars in the CBWS (Chapter 5) might imply that scrape marking does not have a territorial function, but instead signals the presence of individuals to each other.

Insufficient field signs were available to deduce which species of cat produced the scrapes. Often scrapes were the only field signs of large cats found along a trail (particularly during the dry season). Occurrences of footprints in or close to scrapes were rare. Rabinowitz & Nottingham (1986) stated that jaguar scrapes were ~37 cm long (18-58 cm, $N = 26$), 10 cm wide (7-19 cm, $N = 21$) and puma scrapes were ~20 cm long (12-32 cm, $N = 6$), 12 cm wide (6-18 cm, $N = 6$). They do not state which criteria were used to distinguish scrapes. The overlap between these dimensions does not enable distinctions to be made between jaguar and puma scrapes without additional evidence. In this study the hypothesis that scrape dimensions have a bimodal distribution was tested to determine whether there was evidence indicative of size differences between jaguar and puma scrapes.

The function of scrape marks was explored in this chapter by investigating the relationship between the frequency of jaguar and puma captures and the frequency of scrapes along trails. It was not known a priori whether scrape marks have the same function in both species. It was assumed that there was enough heterogeneity in jaguar and puma captures along different survey trails to distinguish between the two species. Three hypotheses were tested for the total dataset of cats irrespective of species and for the two species separately:

1) **Presence hypothesis:** Cat capture rate is directly proportional to scrape rate.

Cats use scrapes to signal their presence in an area, perhaps to indicate presence for hunting, advertising that the area is currently in use or to signal sexual receptiveness to potential mates. The scrapes do not signal territorial marking under this hypothesis: Cat capture rate is directly proportional to scrape rate. Scrape activity of one individual does not influence the scrape activity of other individuals. The spatial distribution of scrapes can be regularly or random, created by multiple individuals scraping independently at regular or random intervals. Clustering of scrapes in certain locations are not expected.

2) **Response hypothesis:** Number of individuals is directly proportional to number of scrapes.

Scrapes are used as territorial markers to temporarily defend an area or resource. The most recent scrape signals which cat is the present occupier. Scraping activity increases in response to other conspecifics in the area and so it is expected that scrapes will be spatially clustered.

3) **Dominance hypothesis:** Capture rate of dominant individuals is directly proportional to scrape rate and/or number of dominant individuals is directly proportional to number of scrapes. Only dominant individuals scrape, either to signal presence in an area to defend a territory. Scrape frequency does not vary with the presence of subordinate individuals. Spatial distribution of scrapes is dependent on the function of scrapes for the dominant individuals either presence or response (see above 1) and 2) for spatial distribution).

The objectives of this chapter are:

1) to investigate the relation between jaguar and puma capture frequency and scrape frequency along trails in the CBWS.

2) to test whether the dimensions of scrapes found in the CBWS have a bimodal distribution indicative of size difference between jaguar and pumas scrapes.

## Methods

Weekly surveys for scrapes were conducted in seven locations. Two researchers walked slowly along fixed trails scanning for scrape marks of large cats. Table 9.1 shows the trail length, the number of camera traps, the survey length and start date. Two surveys were conducted on the western trail during different periods, the first covered a greater length than the second.

Table 9.1 Logistics of scrape surveys. Existing trails are old logging roads, cut trails were specifically cut for this study.

| **Trail name** | **Start date** | **cut/existing trail** | **Length of trail (m)** | ***N* cameras** | ***N* weeks** |
|---|---|---|---|---|---|
| **1** Western (12K) 2003 | 30-Mar-03 | existing | 10282 | min4/max7 | 26 |
| **2** Antelope | 29-Dec-03 | existing | 3747 | 3 | 7 |
| **3** Outlier | 01-Jan-04 | existing | 1892 | 1 | 6 |
| **4** Juan Branch | 13-Jan-04 | existing | 3860 | 4 | 5 |
| **5** Mexican Branch | 01-Jun-04 | existing | 2324 | 6 | 6 |
| **6** Western (6K) 2004 | 28-Sep-04 | existing | 4434 | 6 | 6 |
| **7** 6Kline | 22-Jul-04 | cut | 1721 | 19 | 9 |
| **8** Mitchell Creek | 22-Dec-04 | cut | 2594 | 19 | 5 |

A scrape was recognisable as a raking across the ground with a pile of dirt at one end (Figure 9.1). Two types of scrapes were encountered: either doubling rakings, with a partition, as shown in Figure 9.1, or single rakings, without partition. It is hypothesised that the double rakings were created by scraping with both of the hind feet, as shown in Figure 9.2. This rare photograph shows a jaguar scraping the ground with its hind feet. The scrape was subsequently found to be double raking. Photographic evidence of scraping behaviour was also obtained for pumas (Figure 9.3). It is hypothesised that single rake scrapes are produced with a single front foot. A video camera trap on the Western trail filmed a puma scraping with its front foot. The scrape was subsequently found to be a single raking.

When a scrape was encountered during a survey it was marked with a small broken twig to avoid repeated measures in subsequent weeks. It was always possible to check the identity of a scrape, by reference to measurements of previous weeks if the twigs were tampered with (distance from marker, orientation of scrape, length and width and signs of freshness of scrape).

Scrapes found subsequent to the first survey week could be attributed to cats scraping during the previous week. The following variables were recorded for every scrape:

**1) Partition**: Presence/absence of partition.

**2) Location:** When a scrape was found, a unique tag was placed around the nearest tree and the distance (cm) was recorded between the edge of the scrape and the marker-tree. New marker trees were used for every new scrape except when subsequent scrapes were found within a measurable distance (10 m) from a previous marker-tree. The UTM coordinates were recorded of every marker-tree and the distance between marker trees was measured in paces (~60 cm) by the author. Pacing was more reliable than using UTM coordinates because of the low accuracy of the GPS measures beneath the forest canopy.

**3) Age**: The age of the scrape was estimated, based on degradation of the scrape (smoothness of edges, leaves fallen on top, looseness of dirt). Three age classes were used: old ( > 1week; this category was only used during the first week of survey), medium (2-7 days) or fresh (≤1 day). The accuracy of the fresh category was corroborated by finding scrapes that were positively identified as new when walking the same trail the next day or even the same day, walking back. The other scale rankings were based on general degradation through time of these new scrapes.

**4) Dimensions**: The length (excluding the dirt pile) and width of the scrape were measured from the outside edges where the soil was disturbed.

**5) Direction:** It was assumed that the orientation of the scrape would reflect the direction of walk of the cat, with the dirt pile at the end from which the cat had come.

**6) Scats**: The presence or absence of scats in scrapes was recorded.

Figure 9.1 A scrape of a large cat in the CBWS. A rake across the ground with a pile of dirt at one end (right side). The scrape shows a partition in the middle. A marker pen was included in the photograph to indicate scale.

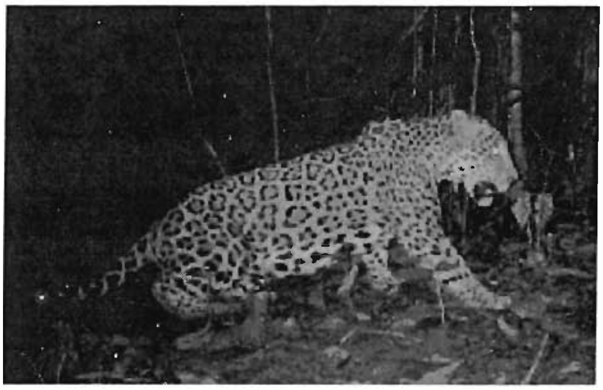

Figure 9.2 A jaguar scraping on the ground with its hind feet. Subsequently a scrape with a partition was found in front of the camera trap.

Figure 9.3 A puma scraping on the ground with its hind legs.

## *Spatial distribution of scrapes*

The distances between consecutive scrapes were calculated using a combination of the distance between consecutive marker-trees and the distance of scrapes from individual marker trees. The hypothesis that cats react to scrapes, of conspecifics or their own scrapes, by scraping in close proximity was tested by comparing the frequency distribution of observed distances between scrapes to a random Poisson distribution of distances with a similar mean. A $\chi^2$ tested the observed distribution against the expected random distribution. Visual comparison of the two distributions, indicated if the observed distribution was more clustered (wider tails) or regular (narrower tails) than random expectation. To test whether cats scraped in response to conspecifics, this analysis was repeated for each survey separately for three different time intervals:

1) The distance between a scrape and its closest neighbour produced during the same week (to examine levels of clustering within a week).

2) The distance between a new scrape and its closest neighbour produced during the previous week (to examine longevity of scrape signalling by studying levels of clustering between weeks).

3) The distance between each scrape and its nearest neighbour for the entire survey period (to examine if the cats have preferred locations for scrapes along trails).

Sample size was only adequate to complete these analyses for six of the seven surveys (Antelope survey, Juan Branch survey, Mexican Branch survey, Outlier survey, Western trail 2003 survey and Western trail 2004 survey).

## *Scrape marking activity and cat presence*

The relationship between scrapes and cat presence was investigated by calculating the correlation between scrape production on a trail and cat presence along the trail, as measured by captures on camera. Several measures of cat presence were used: total number of captures, number of male captures, number of female captures, total number of individuals, total number of male individuals and total number of female individuals. Jaguars and pumas did not always walk the entire trail, therefore camera trap records do not represent cat activity along the entire trail (Chapter 6). For this reason only scrapes found within ~1500 paces (~900 m) either side of each camera location were used for the analysis.

Pearson correlations were calculated between the number of scrapes per week, ~900 m either side of each camera location, and each of the cat presence variables (per week) for all of the 7 surveys combined. This was repeated for jaguars and pumas combined and separately. The puma dataset had missing data points since individual identification was not always possible (Chapter 2).

The capture rates of jaguars (per week) were relatively low compared to those of pumas, whilst the number of puma individuals captured per week was relatively low compared to the number of jaguar individuals. In order to increase the variation in both jaguar capture rate and the number of puma individuals the scrape data and the capture data were pooled over time periods of 2 weeks up to 5 weeks. The correlations were calculated between cat presence and number of scrapes per 1 week, per 2 weeks, per 3 weeks, per 4 weeks, per 5 weeks and the entire survey period (each camera location as a data point). A stepwise regression was then performed on the same datasets to estimate the amount of variation in number of scrapes explained by each of cat presence variables.

Pearson correlations were calculated between the presence variables and number of scrapes per week for each species for weeks in which only a single species, either jaguar or puma, was present. To determine whether the relationships between cat presence variables and number of scrapes differed between the surveys, Pearson correlations were calculated between the number of scrapes and each of the cat presence variables for 5 of the 7 surveys separately, using only the original non-pooled data of 1 week. All data were log10 transformed to approximate a normal distribution for all correlation using Minitab version 14. .

## Scats and cat presence

Pearson correlations were calculated between the number of scats per week, found ~900 m either side of each camera location and each of the cat presence variables (per week) for all of the 7 surveys combined. This was repeated for jaguars and pumas combined and separately. All data were log10 transformed to approximate a normal distribution for all correlations using Minitab version 14.

### *Scrape dimension and form*

The frequency distributions, mean and standard deviations of the lengths and widths of scrapes with and without partitions were calculated to determine if there was any evidence of a bimodal distribution. A bimodal distribution might indicate that jaguar scrapes differed in dimension to puma scrapes. Pearson correlations were calculated between the cat presence variables per weeks and the number of scrapes with partitions and without partitions per week. All data were log10 transformed to approximate a normal distribution for all correlations using Minitab version 14.

## Results

Scrape frequency was up to 40 times higher on the established trails than on the freshly cut trails (Table 9.2). Of the total 445 scats, 265 were found in a scrape, 85 were not found in scrape and the origin of the remaining 95 was unknown in respect to scrapes. It is not clear whether the scats were more frequently deposited in scrapes than not, or whether it was easier for the researcher to detect scats when they were in scrapes.

Table 9.2 Mean number of scrapes and scats identified per week per km during 8 surveys. Western (6K) 2003* is a sub-sample of Western (12K) 2003 for comparison with the Western (6K) 2004 survey.

| **Survey areas** | **Survey weeks** | **Survey length km** | **Total number of scrapes** | **Mean scrapes per week/per km** | **Number of scats in scrape** | **Total number of scats** | **Mean scats per week/per km** |
|---|---|---|---|---|---|---|---|
| Western (12K) 2003 | 26 | 10.28 | 812 | 3.04 | 54 | 88 | 0.33 |
| Western (6K) 2003 * | 26 | 4.43 | 250 | 2.17 | 19 | 32 | 0.28 |
| Western (6K) 2004 | 6 | 4.43 | 250 | 9.40 | 7 | 10 | 0.38 |
| Juan Branch | 5 | 3.86 | 171 | 8.86 | 8 | 8 | 0.41 |
| Antelope | 7 | 3.75 | 143 | 5.45 | 5 | 6 | 0.23 |
| outlier | 6 | 1.89 | 75 | 6.61 | 0 | 0 | 0.00 |
| Mexican Branch | 6 | 2.32 | 50 | 3.59 | 0 | 0 | 0.00 |
| 6 Kline | 9 | 1.72 | 0 | 0.00 | 0 | 2 | 0.13 |
| Mitchell Creek | 5 | 9.26 | 13 | 0.28 | 1 | 1 | 0.02 |

Temporal variation in marking activity was noted for the area with the longest survey record (26 weeks, Western trail) without noticeable relation to season (Figure 9.4).

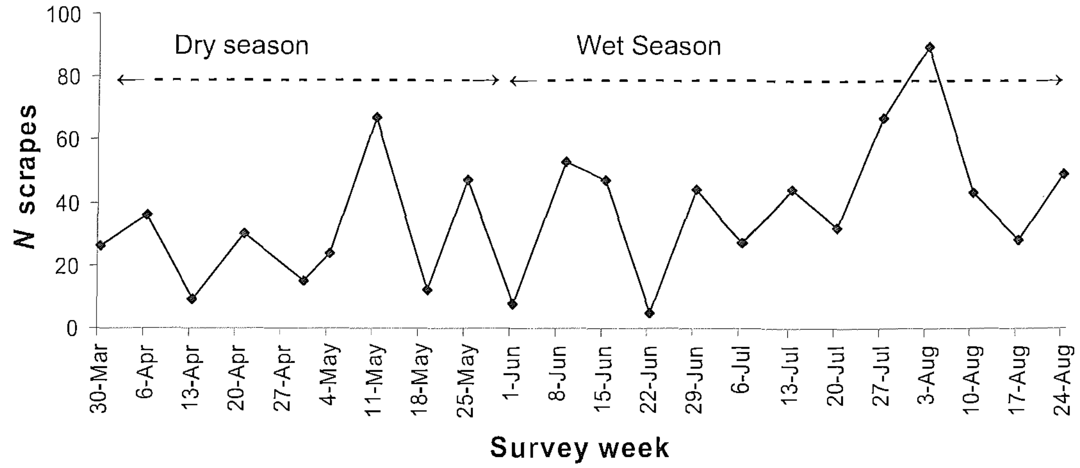

Figure 9.4 Number of scrapes per week along a 10 km trail in the CBWS during 2003.

## *Spatial distribution of scrapes*

The distributions of the observed distances between scrapes was significantly different from Poisson random expectations ($X^2 > 50$, d.f. = 22, $p < 0.01$). Figure 9.5 shows the example of the Western trail survey in 2004. The distributions of the other five surveys were similar as Figure 9.5. All distributions showed a clumped pattern, indicating that scrapes were found in clusters. Most scrapes produced during any given week were produced within 0-10 paces (or 0-6 m) of each other (Figure 9.5a). This distribution shows that the cats react to the presence of other scrapes by scraping in close proximity. Although clustering was less, a similar pattern was found for distances between consecutive scrapes that were produced 1 week apart (Figure 9.5b). It should be taken into account that there were large differences in sample sizes of scrapes between weeks with the result that small numbers of scrapes in some weeks where compared with large numbers the week after. This artificially increased the distance between scrapes between weeks. There was nevertheless a substantial level of clumping. This suggests that cats respond to scrapes produced up to a week previously. Figure 9.5c shows that the distribution of scrapes was clustered in a similar way over the entire survey period, indicating that cats tended to scrape at particular locations along the trail such that scrape activity was more intense at specific "hot-spots". The observed spatial clustering of scrapes could be caused by a single individual marking repeatedly in the same localised area or by conspecifics responding to the scrapes of other individuals by counter-scraping at the same location.

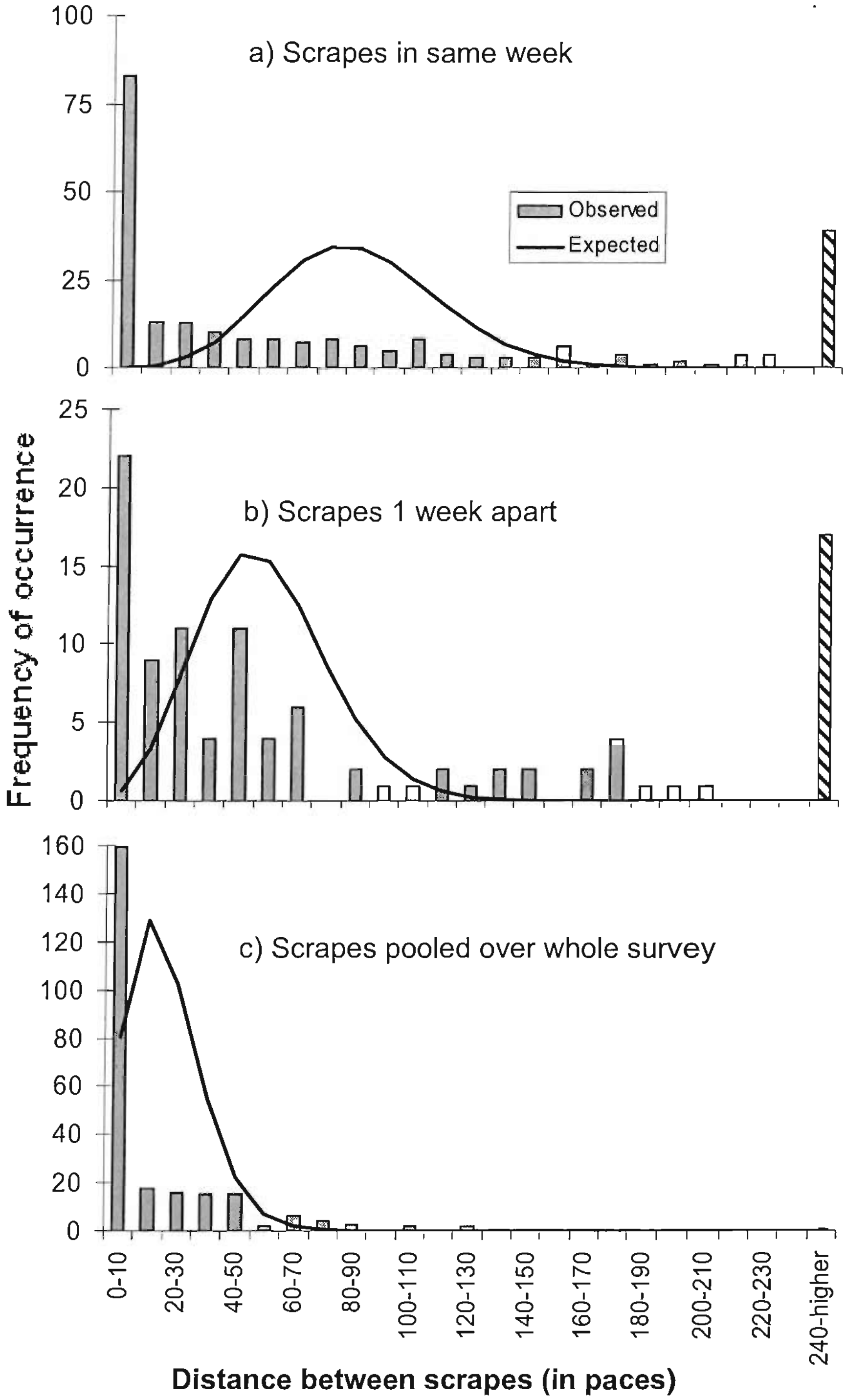

Figure 9.5 Frequency distribution of distances between scrapes along the Western trail (2004 wet season) compared with Poisson random. The trail was surveyed every week for 6 weeks. The hatched bars represent scrapes > 250 paces ( a) maximum = 1136 paces, b) maximum = 994 paces).

## *Scrape marking activity and cat presence*

Cat presence was positively correlated with the number of scrapes around the particular camera location per week, 2 weeks, 3 weeks, 4 weeks, 5 weeks and entire survey length for log10 transformed data (Table 9.3). The strength of the correlations increased the longer the time period over which the data were pooled. Over long periods (entire surveys, 5 weeks and 4 weeks) the number of jaguar individuals were most strongly correlated with scrape numbers; but over shorter periods (3 weeks, 2 weeks, 1 week) the number of puma captures were more strongly correlated with the number of scrapes. Male captures and individuals were more strongly correlated with number of scrapes than were female captures of either cat species. The number of scrapes showed higher correlations for pumas especially for the shorter periods. This suggests that male pumas were more likely to have produced these scrapes. The scatter plots for relations between jaguar and pumas and scrapes were examined for potential non-linear relations. None of the plots indicated clear non-linear relations that were worth pursuing further.

Table 9.4 shows that the variables for jaguars added between 5%-10% explanatory value above the puma value, except for the 4 weeks period and the complete dataset for which jaguar variables were used as the first input variable due to their higher correlation. This indicated that the additional presence of either cat added little extra unique explanatory value to explain scrape variation.

Table 9.3 Pearson correlation between log10 number of scrapes around a camera location (1500 paces either side) and log10 cat presence per camera for jaguars, pumas and both cats combined. Capt. = number of captures, Ind. = number of individuals, separated for total numbers, number of males and females. The scrape and capture data are correlated across different time periods (the total survey datasets, 5 weeks, 4 weeks, 3 weeks, 2 weeks, 1 week). Correlations with $p < 0.05$ are shown in bold.

| | | | **Scrapes combined for analysis per:** | | | | | |
|---|---|---|---|---|---|---|---|---|
| | | | **Total**<br>*N*=18 | **5 weeks**<br>*N*=23 | **4 weeks**<br>*N*=28 | **3 weeks**<br>*N*=38 | **2 weeks**<br>*N*=61 | **1 week**<br>*N*=117 |
| jaguars | **Capt.** | **Total** | **0.67** | **0.49** | **0.41** | 0.21 | **0.31** | **0.20** |
| | | **Male** | **0.68** | **0.41** | **0.38** | 0.18 | **0.29** | 0.16 |
| | | **Female** | 0.24 | 0.22 | 0.22 | 0.14 | 0.15 | **0.18** |
| | **Ind.** | **Total** | **0.76** | **0.55** | **0.47** | 0.24 | **0.33** | **0.19** |
| | | **Male** | **0.76** | **0.46** | **0.44** | 0.21 | **0.31** | 0.14 |
| | | **Female** | 0.26 | 0.23 | 0.22 | 0.15 | 0.15 | **0.18** |
| Puma | **Capt.** | **Total** | **0.73** | **0.55** | **0.46** | **0.60** | **0.53** | **0.54** |
| | | **Male** | **0.72** | **0.50** | **0.42** | **0.56** | **0.40** | **0.55** |
| | | **Female** | **0.43** | 0.17 | 0.01 | 0.28 | 0.07 | **0.18** |
| | **Ind.** | **Total** | **0.57** | 0.36 | 0.22 | **0.34** | **0.30** | **0.49** |
| | | **Male** | **0.54** | 0.26 | 0.20 | 0.29 | **0.27** | **0.49** |
| | | **Female** | **0.55** | 0.20 | 0.02 | 0.29 | 0.06 | 0.14 |
| both cats | **Capt.** | **Total** | **0.84** | **0.75** | **0.57** | **0.62** | **0.59** | **0.54** |
| | | **Male** | **0.88** | **0.60** | **0.43** | **0.48** | **0.43** | **0.50** |
| | | **Female** | **0.52** | 0.32 | 0.10 | **0.37** | 0.12 | **0.25** |
| | **Ind.** | **Total** | **0.67** | 0.43 | 0.29 | **0.37** | **0.34** | **0.46** |
| | | **Male** | **0.72** | 0.35 | 0.27 | 0.30 | **0.29** | **0.40** |
| | | **Female** | **0.60** | 0.37 | 0.19 | **0.38** | 0.12 | **0.23** |

Table 9.4 Stepwise regression: Dependent variable = number of scrapes. Independent variables = jaguar and puma total captures (Jag.Tot.cap./Puma Tot.cap.), jaguar and puma male captures (Jag.Male Cap./ Puma Male Cap.), jaguar and puma female captures (Jag.Fem.Cap./Puma Fem.Cap.), jaguar and puma total individuals (Jag.Tot.Ind./Puma Tot.Ind.), jaguar and puma male individuals (Jag. Male Ind./Puma Male Ind.), jaguar and puma female individuals (Jag.Fem.Ind./ Puma Fem.Ind.). Alpha to enter and remove at 0.15. The stepwise regression repeated pooled datasets over different time periods.

| *N*=23 | | 5weeks | |
|---|---|---|---|
| **Step** | **1** | **2** | **3** |
| **Constant** | 0.75 | 0.52 | 0.19 |
| **Puma Tot.Cap.** | 0.78 | 0.71 | 1.18 |
| *t*-value | 3.03 | 3.14 | 4.19 |
| *p*-value | 0.01 | 0.01 | 0.00 |
| **Jag.Tot.Cap.** | | 0.47 | 0.51 |
| *t*-value | | 2.73 | 3.28 |
| *p*-value | | 0.01 | 0.00 |
| **Puma Fem.Cap.** | | | -0.55 |
| *t*-value | | | -2.42 |
| *p*-value | | | 0.03 |
| S | 0.22 | 0.19 | 0.17 |
| $r^2$ | 0.27 | 0.44 | 0.55 |

| *N*=28 | | 4weeks | |
|---|---|---|---|
| **Step** | **1** | **2** | **3** |
| **Constant** | 1.00 | 0.75 | 0.58 |
| **Jag.Tot.Ind.** | 0.59 | 0.43 | 0.35 |
| *t*-value | 2.68 | 1.89 | 1.63 |
| *p*-value | 0.01 | 0.07 | 0.12 |
| **Puma Tot.Cap.** | | 0.45 | 0.83 |
| *t*-value | | 1.84 | 2.85 |
| *p*-value | | 0.08 | 0.01 |
| **Puma Fem.Cap.** | | | -0.57 |
| *t*-value | | | -2.13 |
| *p*-value | | | 0.04 |
| S | 0.25 | 0.24 | 0.22 |
| $r^2$ | 0.19 | 0.25 | 0.35 |

| *N*=38 | 3weeks | |
|---|---|---|
| **Step** | **1** | **2** |
| **Constant** | 0.62 | 0.48 |
| **Puma Tot.Cap.** | 0.85 | 0.87 |
| *t*-value | 4.53 | 4.91 |
| *p*-value | 0.00 | 0.00 |
| **Jag.Tot.Ind.** | | 0.34 |
| *t*-value | | 2.22 |
| *p*-value | | 0.03 |
| S | 0.25 | 0.23 |
| $r^2$ | 0.35 | 0.41 |

| *N*=61 | 2weeks | |
|---|---|---|
| **Step** | **1** | **2** |
| **Constant** | 0.61 | 0.47 |
| **Puma Tot.Cap.** | 0.74 | 0.77 |
| *t*-value | 4.77 | 5.34 |
| *p*-value | 0.00 | 0.00 |
| **Jag.Tot.Cap.** | | 0.42 |
| *t*-value | | 3.29 |
| *p*-value | | 0.00 |
| S | 0.28 | 0.26 |
| $r^2$ | 0.27 | 0.37 |

| *N*=117 | | 1week | |
|---|---|---|---|
| **Step** | **1** | **2** | **3** |
| **Constant** | 0.43 | 0.37 | 0.38 |
| **Puma Male Cap.** | 0.92 | 0.93 | 0.92 |
| *t*-value | 7.17 | 7.42 | 7.46 |
| *p*-value | 0.00 | 0.00 | 0.00 |
| **Jag.Tot.Cap.** | | 0.33 | 0.97 |
| *t*-value | | 2.56 | 2.69 |
| *p*-value | | 0.01 | 0.01 |
| **Jag. Male Ind.** | | | -0.80 |
| *t*-value | | | -1.91 |
| *p*-value | | | 0.06 |
| S | 0.29 | 0.28 | 0.28 |
| $r^2$ | 0.30 | 0.33 | 0.35 |

| *N*=18 | **Complete dataset** | |
|---|---|---|
| **Step** | **1** | **2** |
| **Constant** | 1.01 | 0.71 |
| **Jag.Male Ind.** | 0.82 | 0.58 |
| *t*-value | 4.65 | 3.71 |
| *p*-value | 0.00 | 0.00 |
| **Puma Male Cap.** | | 0.57 |
| *t*-value | | 3.24 |
| *p*-value | | 0.01 |
| S | 0.18 | 0.14 |
| $r^2$ | 0.55 | 0.71 |

Male puma presence was positively correlated with the numbers of scrapes in weeks when jaguars were absent; but jaguar presence was not positively correlated with the number of scrapes produced in weeks when pumas were absent (Table 9.5, for log10 transformed data). This concords with the previous results that male pumas are the main producers of scrapes. The sample size for jaguar-only weeks was lower than puma only weeks (*N* jaguar = 19, *N* puma = 48).

Table 9.5 Pearson correlation between log10 number of scrapes per week around a camera location (1500 paces either side) and log10 cat presence on the camera per week. Capt. = number of captures, Ind. = number of individuals, separated for total numbers, number of males and females. "Jaguar scrapes" includes data with weeks when only jaguars were registered on camera and "Puma scrapes" includes data when only pumas were registered on camera. *N* jaguar weeks = 19, *N* puma weeks = 48. Correlations with $p < 0.05$ are in bold.

| | | **Jaguar scrapes** | **Puma scrapes** |
|---|---|---|---|
| **Capt.** | **Total** | 0.17 | **0.43** |
| | **Male** | 0.03 | **0.42** |
| | **Female** | 0.23 | 0.20 |
| **Ind.** | **Total** | 0.06 | 0.12 |
| | **Male** | -0.15 | -0.07 |
| | **Female** | 0.23 | 0.13 |

The correlations between cat presence and number of scrapes in the separate survey areas (Table 9.6) showed a similar pattern to the pooled data (Tables 9.3). Puma presence was positively correlated with the number of scrapes produced per week. The Juan Branch survey was an exception, where the presence of female jaguars was also positively correlated with number of scrapes. This can be attributed to a single capture of a female jaguar in this survey during the week of the highest scraping frequency.

There was no evidence that high numbers of scrapes per survey were associated with the presence of certain individual jaguars or pumas. This suggests that scraping was not only limited to dominant individuals.

Table 9.6 Pearson correlation between log10 number of scrapes per week around a camera location (1500 paces either side) and log10 cat presence on the camera per week for 5 of the 7 survey areas. Capt. = number of captures, Ind. = number of individuals, separated for total numbers, number of males and females. Correlations with $p < 0.05$ are in bold.

| | | | **Antelope** | **Juan Br** | **Mexican** | **West(2003)** | **West(2004)** |
|---|---|---|---|---|---|---|---|
| | | | *N*=14 | *N=20* | *N=21* | *N*=64 | *N=20* |
| **Jaguar** | **Capt.** | **Total** | 0.18 | -0.08 | -0.07 | 0.11 | 0.33 |
| | | **Male** | -0.09 | -0.23 | -0.07 | 0.10 | 0.33 |
| | | **Female** | 0.44 | **0.52** | - | 0.05 | - |
| | **Ind.** | **Total** | 0.14 | -0.05 | -0.07 | 0.12 | 0.35 |
| | | **Male** | -0.09 | -0.24 | -0.07 | 0.10 | 0.35 |
| | | **Female** | 0.42 | **0.52** | - | 0.05 | - |
| **Puma** | **Capt.** | **Total** | **0.62** | **0.55** | 0.28 | **0.55** | **0.44** |
| | | **Male** | **0.60** | **0.65** | 0.28 | **0.57** | 0.39 |
| | | **Female** | - | 0.17 | - | 0.16 | - |
| | **Ind.** | **Total** | **0.66** | **0.48** | 0.29 | **0.54** | 0.24 |
| | | **Male** | **0.63** | **0.57** | 0.29 | **0.54** | 0.25 |
| | | **Female** | - | -0.07 | - | 0.22 | - |
| **Tot cats** | **Capt.** | **Total** | 0.45 | 0.51 | 0.21 | **0.52** | **0.46** |
| | | **Male** | 0.21 | 0.45 | 0.21 | **0.51** | 0.42 |
| | | **Female** | 0.22 | 0.37 | - | 0.19 | - |
| | **Ind.** | **Total** | 0.43 | 0.26 | 0.21 | **0.49** | 0.33 |
| | | **Male** | 0.20 | 0.24 | 0.21 | **0.43** | 0.35 |
| | | **Female** | 0.22 | 0.26 | - | 0.25 | - |

## *Scats and cat presence*

Pearson correlations were calculated between the number of scats per week and the cat presence variables per week (Table 9.7). Puma presence had the highest correlation with scat numbers in a similar manner as for scrapes (Table 9.3). Correlations between cat presence variables and scats were weaker than correlations between cat presence and scrapes. The number of scrapes per week was positively correlated with the number of scats per week (Pearson correlation, $r = 0.48, p < 0.01$) therefore the positive relation between scats and captures could be based on the relation between scats and scrapes.

Table 9.7 Pearson correlation between log10 number of scats per week around a camera location (1500 paces either side) and log10 cat presence on the camera per week. Capt. = number of captures, Ind. = number of individuals, separated for total numbers, number of males and females. Correlations with $p < 0.05$ are in bold. ($N$ = 117).

| | | Jaguar | Puma | Total cats |
|---|---|---|---|---|
| | **Total** | 0.01 | **0.34** | **0.27** |
| **Capt.** | **Male** | 0.00 | **0.31** | **0.24** |
| | **Female** | 0.08 | 0.14 | 0.16 |
| | **Total** | 0.04 | **0.29** | **0.25** |
| **Ind.** | **Male** | 0.01 | **0.21** | **0.19** |
| | **Female** | 0.08 | **0.19** | **0.18** |

## *Scrape dimension and form*

Frequency distributions of the lengths and widths of scrapes were unimodal both for scrapes with and without partitions indicating that there were not two distinct groups creating different scrapes (Figure 9.6 and 9.7). There was little difference between the length and width of scrapes with or without partitions, although the differences were significant (Figures 9.6 and 9.7). There were almost twice as many scrapes without partitions as scrapes with partitions, indicating a preference for scraping with the front feet.

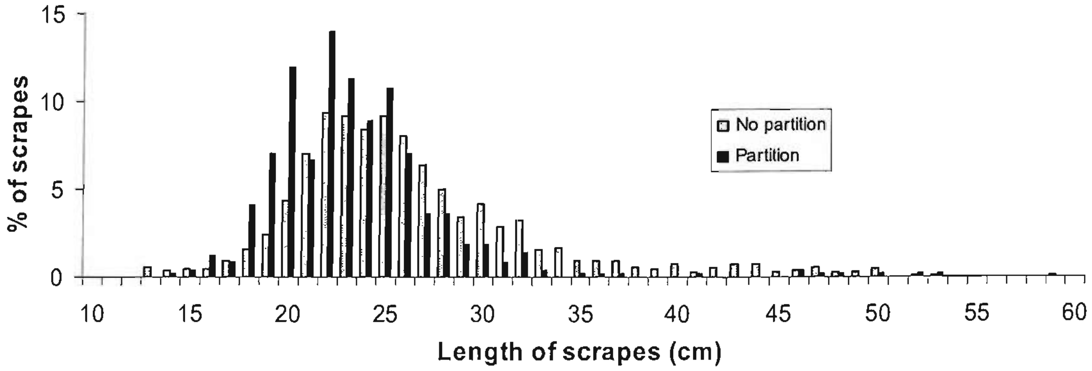

Figure 9.6 Distribution frequency of the length of scrapes combined for all the surveys. The distribution of scrapes with partitions (mean = 23.5 cm, Std Dev. 4.7 cm, $N$ = 495) and without partitions (mean = 26.4 cm, Std Dev. 6.4 cm, $N$ = 824) were significantly different ($t_{1266}$ = -9.39, $p$ < 0.01).

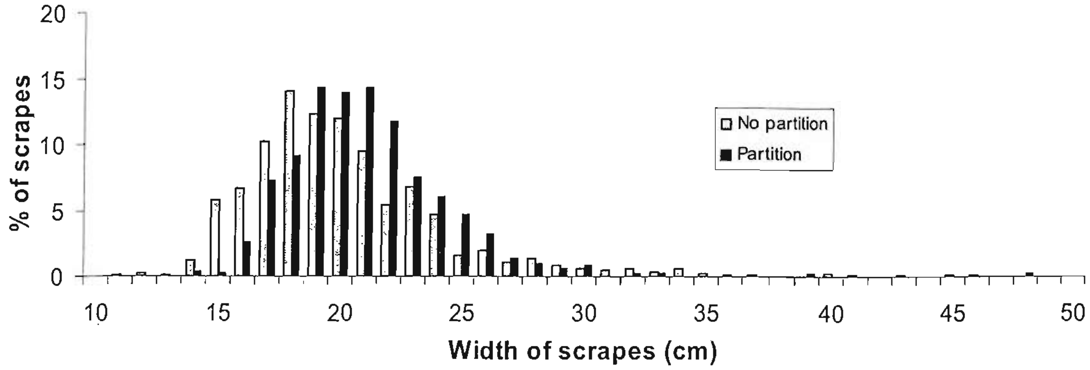

Figure 9.7 Distribution frequency of the width of scrapes combined for all the surveys. The distribution of scrapes with partitions (mean = 21.0 cm, Std Dev. 3.3 cm, $N$ = 495) and without partitions (mean = 20.3 cm, Std Dev. 4.3 cm, $N$ = 824) were significantly different ($t_{1236}$ = 3.65, $p$ < 0.01).

Puma presence variables were more strongly correlated with numbers of either type of scrape than were jaguars (Tables 9.8, for log10 transformed data), indicating a similar pattern of relations as found for correlations of the total dataset (Table 9.3). Partition or non-partition was not more associated with one of the cat species.

Table 9.8 Pearson correlation between log10 number of scrapes per week around a camera location (1500 paces either side) and log10 cat presence at the camera per week for scrapes with partitions and scrapes without partitions. Capt. = number of captures, Ind. = number of individuals, separated for total numbers, number of males and females. Correlations with $p$ < 0.05 are in bold, $N$ = 117.

| | | **Parition** | | | **No partition** | | |
|---|---|---|---|---|---|---|---|
| | | **Jaguar** | **Puma** | **Total cats** | **Jaguar** | **Puma** | **Total cats** |
| **Capt.** | **Total** | 0.08 | **0.40** | **0.33** | **0.20** | **0.50** | **0.51** |
| | **Male** | 0.03 | **0.41** | **0.30** | 0.15 | **0.48** | **0.45** |
| | **Female** | 0.14 | 0.12 | **0.20** | **0.20** | 0.16 | **0.23** |
| **Ind.** | **Total** | 0.09 | **0.42** | **0.32** | 0.19 | 0.37 | **0.38** |
| | **Male** | 0.05 | **0.41** | **0.28** | 0.13 | 0.35 | **0.32** |
| | **Female** | 0.14 | **0.12** | **0.22** | **0.19** | 0.11 | **0.20** |

## Discussion

Scraping on the ground seems to be the most common marking behaviour of the large cats in the CBWS, as observed by Rabinowitz & Nottingham (1986). Marking frequencies of up to 9 scrapes /week / km were recorded, with high variation between areas and through time. The odour of cat urine was occasionally detected near the trails but never directly within scrapes. The frequent rainfall in the rainforest environment probably rapidly removes such sign. Although the majority of scrapes lacked sign of urine or scats, most scats were found in scrapes. It cannot be concluded that most scats are deposited in scrapes since it is likely that scats are simply more cryptic when deposited elsewhere. There was no evidence that jaguar and puma scrapes differ according to the dimensions or form (single or double rake) of the scrape. As such it is difficult to study the species specific function of scrape marks in areas inhabited by both species

Scrapes were spatially clustered, most commonly within 6m of each other regardless of the time period between their production (0 to 26 weeks). This clustering left stretches of the trails with no scrapes. For each cluster, either one individual consistently scrapes in the same location or several individuals scrape in the location where other individuals previously scraped.

The spatial distribution of scrapes rejects the "presence" hypothesis that scrapes function to indicate the presence of an individual who is not influenced by the scrape activity of other individuals. It supports the "response" hypothesis that individuals react to scrapes, either their own scrapes that need to be re-marked at particular locations or to scrapes of other individuals. This pattern of scraping is similar to the territorial marking noted in tigers and in Scottish wildcats (Smith et al. 1989, Kitchener 1991), though it is not consistent with the lack of territoriality in jaguars in the CBWS (see Chapter 5). No information is available on territorial behaviour of pumas in this area.

Scrape marking increased with cat presence (jaguar or pumas) along survey trails, particularly for male puma captures. The weaker correlation of scrape numbers with jaguar presence than with puma presence maybe an artefact of the method of sampling cat presence. Pumas are more likely to walk a trail uninterrupted than are jaguars (Chapter 6). Jaguars may have scraped on the trail but left the trail more often. In future studies cameras should be located according to scrape distribution.

The present study contradicts the original findings of Rabinowitz & Nottingham (1986) that pumas do not scrape in the Cockscomb Basin; rather it suggests that pumas may produce the majority of the scrapes in this area. Seidensticker et al. (1973) suggested that pumas use scraping as their main method marking. Emmons (1987) found that pumas scraped frequently and regularly along trails while jaguars scraped in clusters with longer time intervals between these scraping bouts. The one photograph of a scraping jaguar shows that jaguars do scrape. The scrape was produced by a large mature male. No conclusion can be drawn on the percentage of scrapes that can be assigned to jaguars compared to pumas due to their differential use of trails.

There was no clear evidence that puma scraping behaviour increased when other individuals were present. Puma capture rate and number of individuals were similarly correlated with the number of scrapes. The number of individual pumas walking the trails was low (Chapter 6.) This could mask the correlations between individuals and scrape levels and so it is difficult to draw conclusions about the territorial function of scrapes from the present dataset.

No evidence was found to support they hypothesis that scrape marking is related to dominance. The dataset was scanned for increases in scrape activity associated with particular individuals but no such relation was found for any of the individuals (jaguar or puma).

The spatial distribution of scrapes and the relationships between puma presence and scrape activity suggest that the reaction hypothesis without dominance best explains the scraping behaviour of pumas in the CBWS. The function of jaguar scrape-marking behaviour is less clear.

## Recommendations

If scats found in scrapes can be assigned to species then further analysis is possible of the frequency of scrapes associated with either species. Future studies should identify scrape "hotspots" along the trail and deploy cameras in these areas rather than distribute them evenly along the trail. A pilot study creating artificial scrapes with scats from zoo jaguars along the trail elicited minimal response. The present study suggests that this kind of experiment should be repeated with puma scats.

# Chapter 10

# General discussion

## Introduction

Planning conservation strategies for elusive mammals that live at low density such as jaguars is hindered by lack of knowledge about their local abundance and ecology. Obtaining such data requires the development of reliable methods to estimate abundance. Camera traps are a promising research tool for such studies. Over a 4-year period, 37 individual jaguars have been identified in the CBWS using camera traps, collecting more information than could be otherwise achieved by a telemetry study with similar funding. No other study of jaguars has positively identified a similar number of individuals. The method is not without problems: the accuracy and precision of abundance estimates based on mark-recapture analysis of camera trap data of individually recognisable animals are influenced by low and heterogeneous capture rates of individuals and by the relatively small size of the study area compared to the home range size of wide-ranging species such as jaguars. The aim of this chapter is to evaluate the main results and limitations of this study as a whole, in relation to existing published work on jaguars, leading to future recommendations.

## Low and heterogeneous capture rates

This is the first study to recognise that low and heterogeneous capture rates are the main cause of unreliability in abundance estimates based on camera trap data. Many published studies have used camera trap data to estimate jaguar and tiger abundances (O'Brien et al. 2003, Kawanishi & Sunquist 2004, Maffei et al. 2004, Silver et al. 2004, Maffei et al. 2005, Miller & Miller 2005, Miller 2005). All these studies had low and/or heterogeneous capture rates bringing into question the reliability of the abundance estimates. Future abundance estimates should be based on higher capture rates and attempts made to prevent high heterogeneity in capture rates (see Chapter 3). Such studies must provide information to show that their findings are reliable before the estimates are used for further analysis or directing conservation policy.

Pooling trap occasions together can be used to increase the overall capture rate (Chapter 3) but often this is not enough to resolve a problem of low catchability of specific individuals, in particular the difference in capture rates between males and females results in high capture heterogeneity within the population. The high capture probability of males compared to females is due to behavioural differences between the sexes (see Chapter 5). This is the first study to highlight potential bias in abundance estimates of high male capture rates in camera trap studies. Male-biased captures are not unique to jaguars but are a common phenomenon in trapping studies of mammals from wombats (*Lasiorhinus krefftii*, Banks et al. 2003) to grizzly bears (*Ursus arctos*, Boulanger et al. 2004). Such an inherent source of capture heterogeneity is problematic for mark-recapture analyses and cannot be resolved easily. Until field methodology can be refined to boost female capture rates, male and female abundance could be estimated separately. In this study the number of females captured and their capture rate was too low to estimate female abundance. Future research should focus on increasing female capture rates to allow separate mark-recapture analysis between the sexes.

This study detailed the problem of low and heterogeneous capture rates and provided bounds within which estimates could be considered reliable. The obvious approach to increase capture rates would be to increase the density of camera traps in an area. Chapter 4 showed that doubling the camera trap density by using small creeks and small game trails within the forest did not increase the number of individuals captured, and overall capture rate increased only marginally. This is because capture probability was low away from main trails. Most captures were on the established trail systems (Chapter 4). Maffei et al. (2004) found a similar result for jaguars in the Bolivian Chaco and the high capture rates of tigers (Karanth & Nichols 1998) are based mainly on road systems. Success of camera trapping large cats relies on the fact that the cats will utilise man-made trails as their main travel routes. Camera trapping in undisturbed forest without a trail system will likely suffer from low capture rates, for example studies of tigers in South East Asian rainforest (Kawanishi & Sunquist 2000, O'Brien 2003). Opening trails may be the only way to increase capture rate but it may also increase the accessibility of the study area to hunters; this risk has to be balanced against the conservation goals of the study. The design of the trail system has to be an attractive travelling route for cats e.g. leading to an established trail or a river system. A dense grid of trails connecting several large old logging roads with the main rivers is planned for the interior of the CBWS. The establishment of this trail grid will be studied experimentally by monitoring trail use by cats whilst systematically increasing the number of newly cut trails and camera density. Increases in capture rates will be monitored with specific reference to increases in female capture rate.

## Area of the study

The study area covered by camera traps is usually limited by the logistics of camera maintenance, rather than based on the biology of the target species. White et al. (1982) indicated that the ratio of home range size to study area should be low to reliably estimate abundance using mark-recapture analysis (see Chapter 2). Density estimates of big cats using camera trap data are based on study areas ranging ~150-200 km$^2$ (O'Brien et al. 2003, Kawanishi & Sunquist 2004, Maffei et al. 2004, Silver et al. 2004, Maffei et al. 2005, Miller & Miller 2005, Miller 2005); large enough for relatively few exclusive home ranges. In this study density estimates were consistent for areas ranging100-200 km$^2$ as long as overall catchability was high ($\hat{p} > 0.03$). This suggests that the study area is adequate for estimating jaguar density, probably because of the extensive overlap in home range overlap (see Chapter 5).

Open population models indicated a high rate of emigration and immigration (almost 100%) of jaguars into and out of the study area (Chapter 5). This is probably due to resident individuals with home ranges that only partially overlap with the study area rather than permanent movement into or out of the area. Many individuals captured within the study area do extend their range beyond its boundaries (pers. comm. R Foster, PhD student Southampton University). The high level of movement in and out of the study area increases the heterogeneity in capture rate and lowers the overall capture rates, causing overestimation of abundance.

It can be concluded that heterogeneity in capture rate is more likely in smaller areas due to greater movement into and out of the study area. Increasing the study area will increase the proportion of individuals that are full residents and so decrease the edge effect. This kind of edge effect is well documented in mark-recapture studies of small mammals (Schlesser et al. 2002). The minimum size of study area that can be used for abundance and density estimates needs to be studied experimentally by sub-sampling data from a large-scale survey. Such a survey would be well suited for the study of mean maximum distance moved (MMDM) for the calculation of the buffer strip size, using different sized study areas (see Chapter 2). Such a study would require extensive resources, cameras and man power, to cover an area that is sufficiently large.

The area of this study is probably better suited to estimate the abundance of species with home ranges that are smaller than those jaguars, for example the ocelot. Although the study area may be large enough the camera density needs to be high enough to fulfil the assumption of the closed population model that no individual has a zero capture chance (Chapter 2). The camera spacing in this study is probably too wide to satisfy this assumption. As such, more camera traps are required, either to enlarge the area to study jaguars at similar camera trap density and/or to deploy a higher density of cameras to study ocelots.

Few studies can afford to purchase and maintain more than 40 camera traps, as in this study. The availability of resources for camera trap research could be easily overcome if independent researchers would collaborate, sharing cameras so as to conduct mass surveys simultaneously. In reality researchers working on the same species often compete for limited funding. Camera traps in the tropics have a high break down rate and need to be replaced frequently. Projects should be designed to fund several researchers within the same region with sufficient resources to guarantee that each research site always has enough working cameras available. Collaboration at the regional level is essential to take forward jaguar research and conservation.

## Validation of abundance estimates based on camera trapping

Abundance estimates based on camera trap data need to be validated with independent methods, for example, the combined use of telemetry and camera trapping. Genetic analysis of scats or hair samples may provide an alternative method of validation. Scats collected systematically can be genotyped to the individual level and used for mark-recapture analysis (Lukacs & Burnham 2005). Trained dogs can be used in the field to locate scats and so maximise the data set. Hair traps have successfully collected hair from lynx (*Lynx canadensis*, McDaniel et al. 2000). Scat surveys using trained dogs and systematic hair trap surveys are planned for the CBWS to provide genetic samples for mark-recapture abundance estimates of jaguars. If successful the use of scat or hair samples could reduce the need for expensive field equipment such as camera traps or radio collars. Although not cheap, the cost of genetic analysis is predictable, unlike the cost of camera trap surveys which varies depending on theft and breakdown of cameras; if necessary samples can be collected in advance and stored until funding for genotyping is available. Genetic sampling, rather than photographic sampling, could potentially allow abundance estimates of species which are not individually recognisable, such as pumas.

## Estimating prey abundance and diet studies

Absolute capture rates could not be used as an abundance index of any of the ungulate species in this study because capture probability varied with species and trail type (see Chapter 7). Genetic sampling of individuals, as described in the preceding section, could provide an alternative means of estimating abundance of such species, however the cost of genetic analysis is too high to use this method for all potential prey species. Abundance estimates of prey species require a cheaper, more basic method. No single method can be used to estimate the abundance of all prey species. Species specific methods have to be developed. Research in the CBWS is planned to test the efficacy of different methods (e.g. sign surveys, burrow counts, camera traps) to estimate the absolute abundance of six prey species: armadillo, paca, brocket deer, collared peccary, white-lipped peccary and coatis.

Collection of jaguar and puma scats for genetic analysis provides material for diet analysis. Scat collection in the CBWS will continue, both for genetic and diet analysis. Using one of the largest collections of scats for jaguars and pumas in the neotropics, temporal and spatial variation was detected in the diet over a 3-year period (see Chapter 8). Regular systematic surveys for scats will provide additional data for the analysis of spatial and temporal variation in the diet of jaguars and pumas. This will provide information about the dietary overlap between jaguars and pumas and may contribute to better understanding the mechanism of co-existence of these two species. If genotyping to the individual level is possible then individual variation in diet can be studied.

Individual identification of scats in combination found in scrapes would give detailed information on species and individuals marking along trails. This would provide a detailed picture of marking behaviour not possible for the present study (Chapter 9).

## Estimation of life history parameters

The use of open population models for estimation of life history parameters of cryptic species is promising, for example Karanth et al. (in press) did a detailed study of life history parameters using 10 years of camera trap data for tigers in Nagarahole, in India. This is the first study that attempted to estimate life history parameters (recruitment, survival, emigration and immigration) for jaguars, using 5 years of survey data (Chapter 5). High levels of immigration and emigration were combined with high survival over the 5-year period. The parameters may have been overestimated because the study area was too small. Movement in and out of the study area blurs the distinction between mortality and emigration. The survey should be repeated over several more years in order to accurately estimate survival in relation to emigration and immigration. Alternatively the survey should be repeated over a larger area to reduce the edge effect. Future studies should ensure that the survey design avoids potential bias caused by edge effects.

## The study of jaguar and puma ecology using camera traps

This is the first study to use camera traps for answering ecological questions about the spatial and temporal distribution of jaguars, pumas and their prey. Camera traps are the perfect tool for studying interactions between conspecifics and sympatric species. Previous telemetry studies of jaguars suffer from low sample sizes of individuals (range 2-5) and any information about interactions between individuals comes only from the collared individuals (Schaller & Crawshaw 1980, Rabinowitz & Nottingham 1986, Crawshaw & Quigley 1991, Núñez et al. 2002, Scognamillo et al. 2003). Camera trapping in this study provided data on many more jaguars (37) than in any of the previous telemetry studies. It provided detailed information on activity patterns, not only of jaguars and pumas but also of their prey (see Chapters 6 and 7).

Despite similarity in activity patterns it demonstrated spatio-temporal avoidance between jaguars and pumas (see Chapter 6). Lack of avoidance and territoriality was clearly shown for male jaguars (see Chapter 5). The dataset could be used to answer many other questions, for example, whether ocelots avoid the two larger cats, jaguars and pumas. Camera trap studies can be designed to answer specific questions, for example the level of trail walking of jaguars compared to pumas (see Chapter 6) or the study of scrape marking behaviour (see Chapter 9).

Before the use of camera traps, the study of marking behaviour of jaguars and pumas could only go beyond frequency counts with the aid of telemetry data, allowing inferences of likely candidates for scraping. Rabinowitz & Nottingham (1986) used telemetry data to relate movements of collared male jaguars to changes in scrape frequency without knowledge of other individuals in the area. They concluded, perhaps incorrectly, that jaguars were mainly responsible for scraping. Camera traps gives a less biased record of cat traffic along the trail, and this study suggests that, whilst both species scrape mark, pumas do so more than jaguars. The combination of genotyping scats, camera trapping and telemetry would be ideal for the study of the functions of marking in both cat species. Smith et al. (1989) showed that detailed study of marking behaviour of tigers could provide useful insights into social system of the species. They used sightings, telemetry data and footprints for assigning markings.

The study of habitat use of different species using camera traps was not so successful (see Chapters 4 and 7). This is largely because habitat features were analysed ad-hoc around camera traps placed for different purposes. For systematic habitat analysis cameras should be placed along habitat gradients, e.g. different distances from rivers, streams, trails, human civilisation and up slopes. Capture frequencies along these gradients could reveal habitat preferences for all species that have relatively high capture records. Telemetry data are still superior in studying habitat preferences for single individuals but camera traps can be used, with the advantage that data are gathered on multiple species simultaneously.

## Future work

This thesis is just the beginning: following the work achieved during this research, the Wildlife Conservation Society (WCS) has agreed to support Belize as a model country for jaguar conservation and the CBWS as a long-term study site for jaguar research. Methods to reliably estimate abundance and study the ecology of jaguars will continue to be tested and optimised within the CBWS. Abundance estimates of jaguar and pumas together with information about prey availability and diet preferences of individuals, will give a complete picture of the interaction between these two species in relation to their prey.

Although 46% of Belize is protected, not all of this land is necessarily suitable for jaguars. Often land that is put aside for protection is that which is not desired by farmers or developers, for example mountainous areas. Belizean landowners frequently lay claims to lowland areas arguing that the jaguar has plenty of forest in the protected highlands. There are little data to show that such habitats are suitable for the jaguar. Regular camera trap surveys will continue to monitor the jaguar population in the CBWS and will be extended into the rugged areas to the west. This will allow density estimates in potentially less favourable habitat. Collaborations are planned between research groups within Belize to estimate jaguar abundance in different areas so to produce a countrywide "jaguar density" map. This will identify jaguar hotspots within the country that should be the focus of future conservation efforts.

The CBWS will be the testing ground for the development of methods to estimate absolute abundance of pumas and prey species using a wide variety of techniques from simple sign surveys to genetic sampling combined with mark-recapture analyses. Collection of scats will continue in order to allow long-term monitoring of jaguar and puma diet in and around the CBWS. It will also be useful to monitor and compare diet between different areas within Belize. This will eventually contribute to a better understanding of how diet varies within and between jaguars and pumas depending on habitat and prey availability. The WCS will support Belizean students to conduct small-scale projects; diet studies in different parts of Belize are an obvious candidate for such projects.

An important prerequisite for any successful long-term research site is its long-term security. Daily interaction with the CBWS director and staff alerts us to current threats in and around the park. The WCS is committed to support the CBWS logistically and financially when necessary to curb threats of illegal poaching or extraction.

Most telemetry studies collar whichever individuals are trapped, without any previous knowledge of their history or social status. When interested in specific aspects of ranging behaviour (residents, dispersers etc), long-term camera trap data can focus live-trapping efforts on specific individuals with a known history. Telemetry studies will be carried out in and around the CBWS if specific questions demand detailed individual movement patterns. One aspect that requires such detailed knowledge is movement of jaguars in and out of the protected area. Farmers neighbouring the CBWS regularly kill jaguars to protect their livestock. Research has already begun to discover whether source-sink dynamics exist in this area (pers comm., R. Foster, PhD student, Southampton University) but future work will focus on finding ways to ensure that a stable jaguar population can live alongside cattle farms. Good relations have been established between the WCS and the surrounding farms and villages. This provides a solid basis for taking the research forward to find satisfactory measures of conflict mitigation. It is planned that the human-jaguar conflict program will be expanded nation-wide across Belize, bringing together livestock owners, local NGOs and the Government of Belize.

The WCS plan to support long-term jaguar research in several other geographic regions of the jaguars' range; probably in the Bolivian Chaco and the Brazilian Pantanal or the Venezuelan Llanos floodplains. Comparison of population dynamics and inter- and intra-specific competition between these different regions will give a complete picture of ecological requirements and interactions of the tropical jaguar and puma. Lessons learned about survey methodology from these research sites can be used to implement reliable and quick surveys throughout the jaguar range. This will contribute to a range map of jaguar densities so that conservation efforts can focus on priority areas (for example efforts to connect isolated high density jaguar areas to more contiguous areas where jaguars exist). If research in the CBWS remains successful, the same framework and techniques can be applied to the study of other elusive tropical species.

# Appendix A

# Phylogeny of large neotropical cats

## *Phylogeny of jaguars and pumas*

Jaguars belong to the genus *Panthera* together with four others: lions, tigers, leopards and snow leopards (*Panthera uncia*). Recently there has been debate as to whether the snow leopard belongs to the *Panthera* lineage and it has been proposed that it should be placed in its own genus, *Uncia* (Hemmer 1978, (Herrington 1986, Salles 1992, O'Brien et al. 1996 in Bininda-Emonds et al. 2001), Yu & Zhang 2005, Bininda-Emonds et al. 2001). Sometimes the clouded leopard (*Neofelis nebulosa)* is included in the *Panthera* lineage (O'Brien et al. 1996 in Bininda-Emonds et al. 2001, Yu & Zhang 2005). A distinguishing morphological characteristic of *Panthera* sp. is an elastic ligament in the hyoid apparatus of the throat, a system of small bones that provides support and anchorage for the voice box and tongue. This ligament is generally thought to permit movement and the characteristic roar of these species (Turner & Anton 1997).

In recent years there has bee much debate about the phylogeny of the puma. Chemical signalling compounds produced in faecal material of the *Panthera* lineage are similar, but differ from those of the puma (Bininda-Emonds et al. 2001). It has been associated as a distant relative of the *Panthera* genus together with the cheetah ( Salles 1992 in Bininda-Emonds et al. 2001), and was later described as a member of the *Felis* genus (Collier & O'Brien 1985). It has also been classified in a monophyletic group with the cheetah and the jaguarundi (Johnson & O'Brien 1997, Pecon Slattery et al. 1994, Mattern & Mc Lennan 2000). Most recent evidence from Yu & Zhang (2005) put the puma in close association with the cheetah in a group with golden cats and lynxes.

Eight subspecies of jaguar have been described historically, mainly based on size differences and geographic distribution (see Table 1.2). Individuals from the north (Central American to the northern part of the Amazon basin) have been differentiated from those in the south (southern part of the Amazon basin, Peru and the southern part of their range). However there was evidence of substantial gene flow between these two populations and genetic analysis cannot substantiate any difference between the jaguar populations from different regions (Johnson et al. 2002; Eizirik et al. 2001).

A different pattern of sub-speciation was discovered in ocelot and margay. Both are small cat species of the Americas with similar geographic distributions as jaguars. There are three distinct populations of both species (Central America, northern South America and southern South America) indicating that physical barriers may have isolated these three pockets (Eizirik et al. 1998). Both the ocelot and the margay are thought to be evolutionarily older than jaguars (Eizirik et al. 2001).

Table A.1 The eight subspecies of jaguar described historically (from the IUCN Cat Specialist Group website).

| **Scientific name** | **Range of subspecies** |
|---|---|
| *P. o. arizonensis* | Arizona and northern Mexico |
| *P. o. centralis* | Chiapas, Mexico to Colombia |
| *P. o. goldmani* | Yucatan and northern Guatemala |
| *P. o. hernandesii* | Sonora to Chiapas |
| *P. o. onca* | Venezuela to East and central Brazil |
| *P. o. palustris* | South Bolivia, Mato Grosso, central Argentina |
| *P. o. peruvianus* | Peru |
| *P. o. veraecrucis* | South Texas, north Chiapas |

The IUCN (IUCN Cat Specialist Group website) describes six subspecies of the puma (*P. c. cabrerae, P. c. capricornensis, P. c. concolor, P. c. costaricensis, P. c. cougar, P. c. puma*). Originally 15 subspecies were described that were based on vague morphological differences (Pennisi undated IUCN cat specialist website, report from American Genetic Association, study by O'Brien S. J.). The Pennisi report also states that the Central American pumas are distinct from the Northern pumas and that four South American puma subspecies can be distinguished. The most genetic variation can be found below the Amazon River, suggesting that this was the founder puma population and that from here they migrated north. Unfortunately no information is available on the distribution of the puma subspecies described in relation to the sub-speciation patterns proposed for the ocelot and margay.

# Appendix B

## Individual range behaviour of jaguars

# Individual ranging behaviour

Several maps were produced over different periods to indicate distribution patterns of individuals. Male jaguar M00-1 had the highest number of captures of all individuals photographed in CBWS during the study period (88 captures). M00-1 was first captured as an adult in a pilot study in 2000 and subsequently captured in the first survey of 2002, all throughout 2003 and his final capture was in August 2004. Despite continuous camera trapping in the area there have been no captures of M00-1 to date (October 2006, pers. comm. R. Foster, PhD student, Southampton University). M00-1 was at least 2 years old at first capture and at least 6 years old on last capture. The consistent captures of M00-1, roughly every week, in the north eastern region of CBWS indicated that he was a long term resident. The abruptness of his disappearance suggests that he died, since we have no other evidence of a resident male completely leaving his range in a short space of time. The upper panel of Figure B.1 shows the captures of M00-1 (in red) clearly overlapping with other males. The other males made incursions into the area but the majority of captures in the north east of the CBWS between February 2003 to August 2004 were of M00-1. He was consistently present while many other males at different times occupied the area simultaneously. He made sporadic incursions to the west limits of his range.

Figure B.1 gives evidence of two males responding to the disappearance of M00-1. Throughout the period when M00-1 was present (February 2003 to August 2004) male M03-9 had a low capture frequency all through the area (Figure B.1 black circles), and male M03-7 had a high capture frequency but was confined to the eastern edge of the CBWS (Figure B.1 white circles). After M00-1 disappeared the capture frequency of M03-9 increased throughout the range. He was captured in the same locations as previously but at a higher rate similar to that of his predecessor M00-1. At the same time M03-7 moved west and was captured frequently throughout the previous range of M00-1. It is likely that these increased capture rate of M03-9 and the shift in the range of M03-7 were related to the disappearance of M00-1.

The only region within the study area were a high number of different female jaguars were captured was also in the north east of the CBWS. Five different females were captured in this area between September 2003 and June 2005 (Figure B.2). The map demonstrates the relatively low female capture rate typical of the entire study area. Three females, F02-10, F03-2 and F03-3, were captured throughout the entire period, F04-9 was only captured in April 2004 and F04-14 was first captured in September 2004 and continues to be captured erratically to date (October 2006, pers. Comm. R. Foster, PhD student, Southampton University). The captures of F04-9 coincided with captures of F02-10 in the same month in the same location. There was a high level of overlap between F03-2 and F03-3. There is no evidence that certain females dominate certain areas to the exclusion of other females.

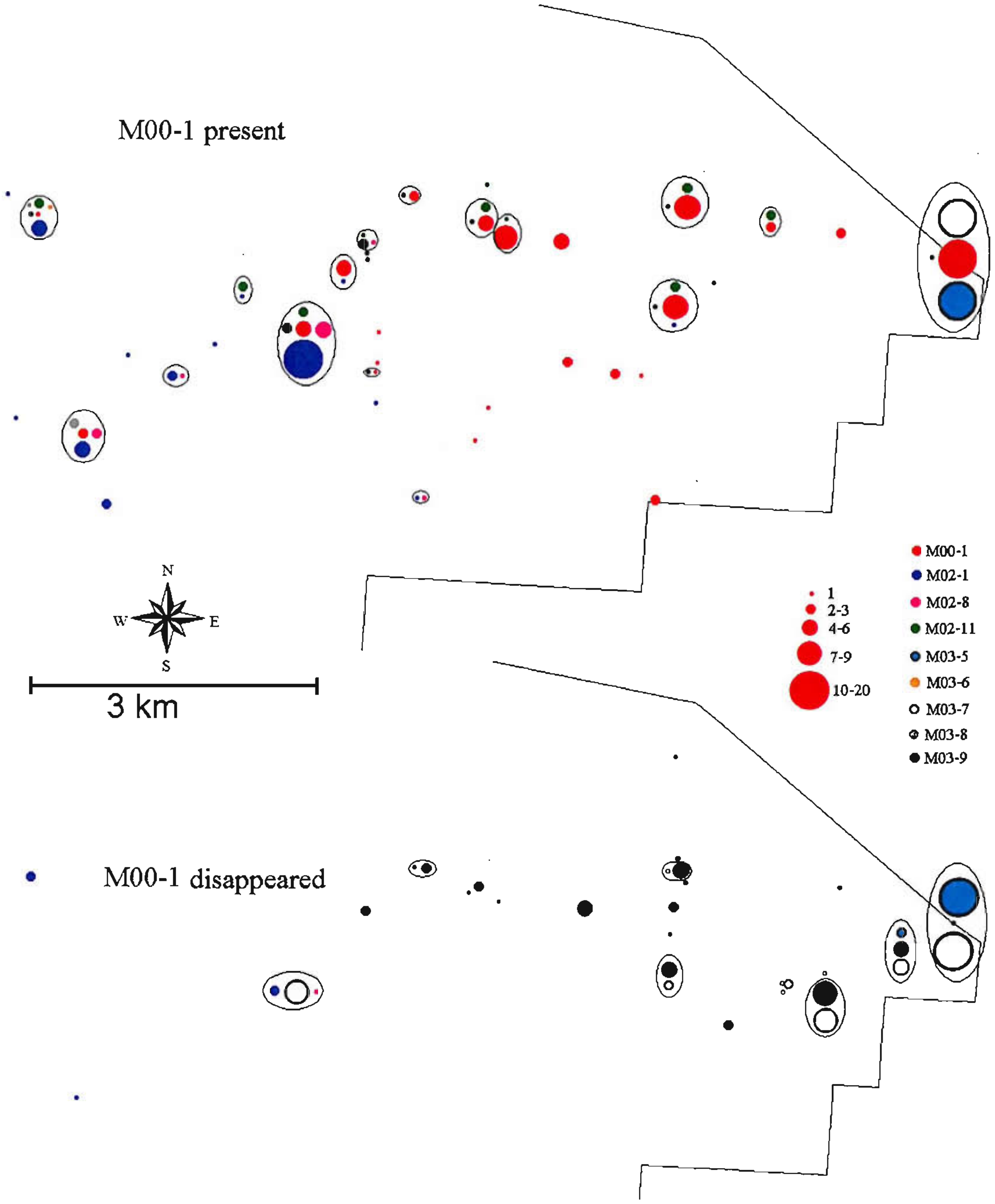

Figure B.1. Captures of male jaguars in the north east region of the CBWS. The upper panel represents the period February 2003-August 2004 and the lower panel represents the period September 2004-June 2005. The area was based on the outer range of male M00-1 (red circles). The size of the coloured circles represents the number of captures for specific individuals (see legend). Grey border surrounding clusters of circles indicates that the captures are in the same location.

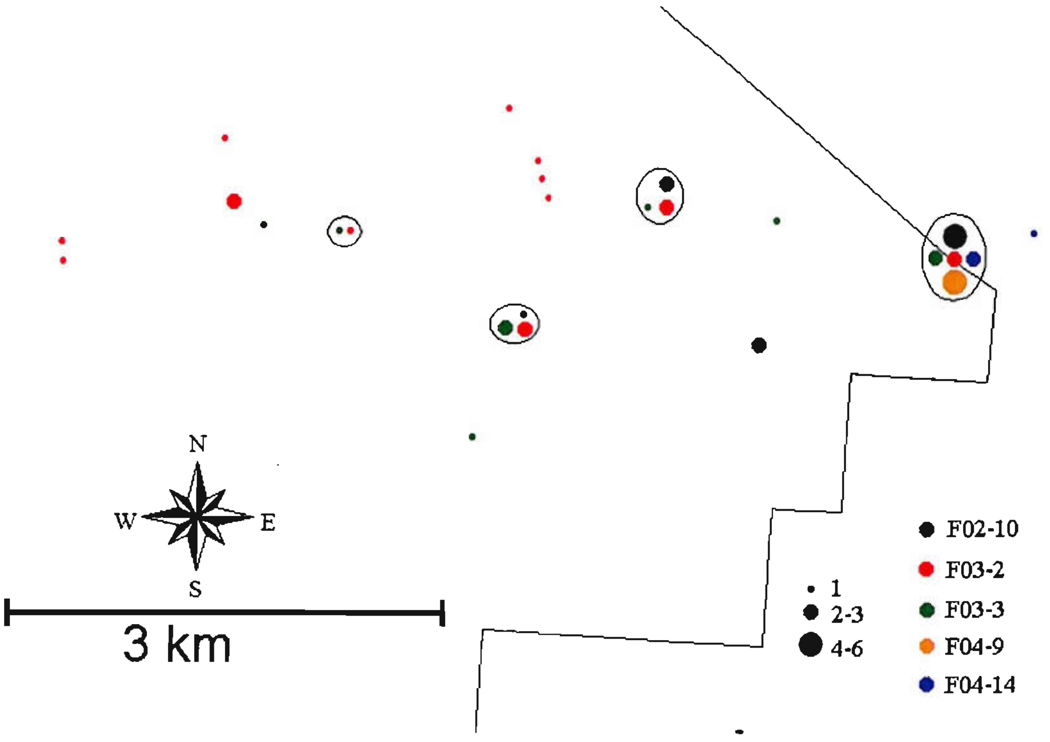

Figure B.2 Female captures in the north east region of the CBWS between September 2003 and June 2005. The size of the coloured circles represents the number of captures for specific individuals (see legend). Grey border surrounding clusters of circles indicates that the captures are in the same location.

The south eastern region of the CBWS showed an annual flux in the range of male jaguars between 2002 and 2005 (Figures A.3 and A.4). The changes were gradual: males slowly moved away from the area (reduced capture rate) as other males became established. The main survey data (see chapter 3) were used for these maps. The 2004 maps also included data from a survey conducted 1 month prior to the main survey. The most eastern camera present in 2004 and 2005 was not used in 2002 and was stolen during the first month of the survey in 2003.

In 2002 male M02-6 was present throughout the region. Male M00-3 and male M02-7 were both present on the western edge. Male M00-3 made a single excursion to the east. Male M02-5 had a low capture frequency in the east together with a single capture of male M02-4.

In 2003 M02-6 remained dominant in the south and widened his range to the south east and to the south west. M02-4 moved throughout the same area as M02-6. M02-4 was wounded after being photographed on the same day as M02-6 on the most western camera. M02-5 remained to the east. The single photograph of M02-8 in this area was taken in December 2003 when a camera was set up in this area for a short period.

In 2004, M02-6 was no longer dominant within his range. His capture rate fell and equilibrated with the capture rate of M02-4. To the west M02-6, M02-4 and M00-5 had equal capture rates. M02-8 and M02-2 moved into the east and M02-5 became the dominant male here. He may already have been dominant in 2002 and 2003 but the eastern camera was not there to register this.

By 2005 a new male jaguar, M05-1, had moved into the west, M02-4 had disappeared and M02-6 had shifted far to the west. M02-8 seemed to have established himself in the east although the far east was mainly occupied by M02-5. This was the only location that never had a reversal or a change in dominance (Table 5.5). The majority of captures every month were of M02-5. It was noted that M02-5 his range extended further south and out of the CBWS in 2006 (pers. comm. R. Foster, PhD student Southampton University) and he seemed to be the male with the highest capture rate in this region. In March 2006 M02-4 and M02-6 were no longer present, but M02-04 returned in October in the north east of the CBWS, (pers. comm. R. Foster, PhD student, Southampton University).

No other regions of CBWS within the study area showed any shifts in occupation. High numbers of individuals were captured in the middle and the north of the study area but all with relatively low capture rates.

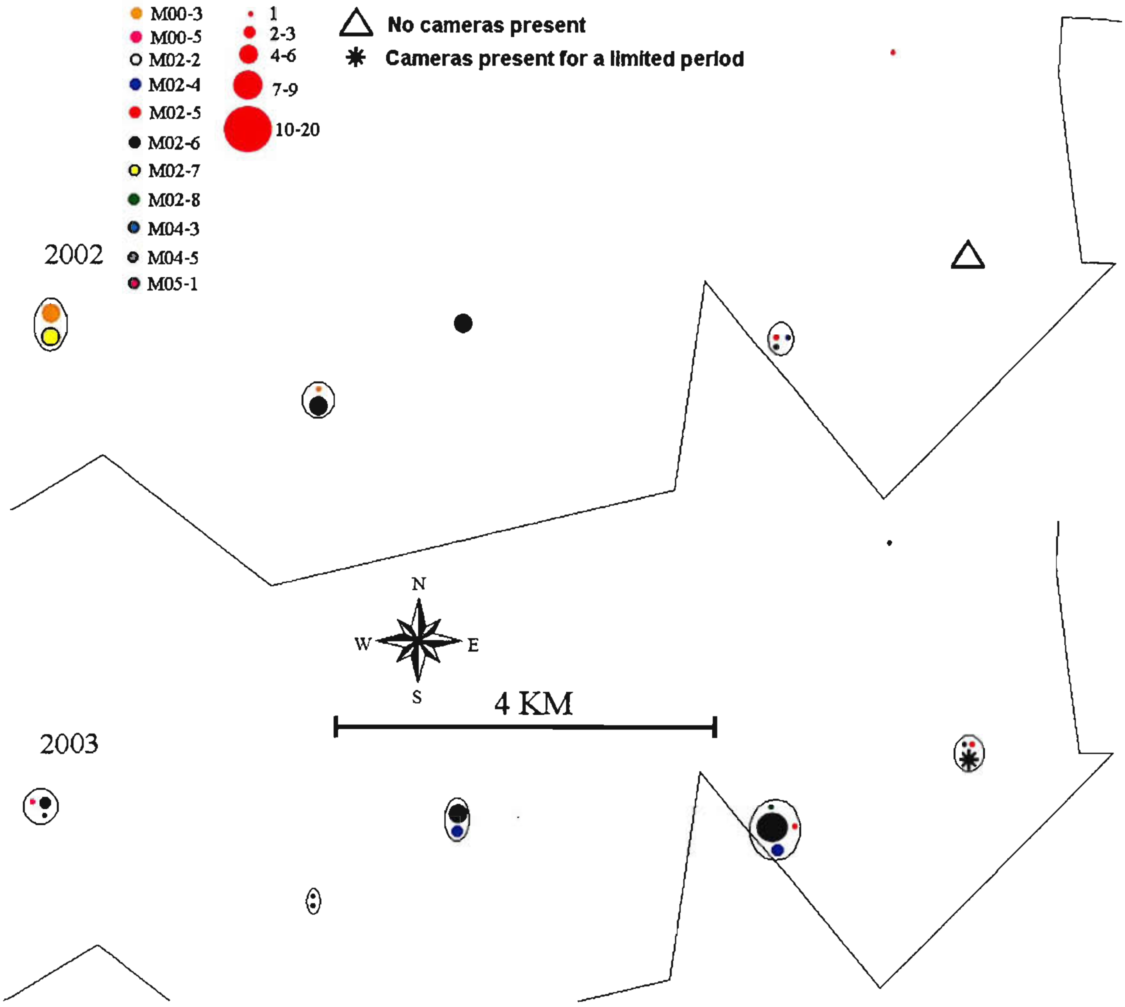

Figure B.3 Male jaguar captures in the south east region of the CBWS. The upper panel shows the captures for the year 2002 and the lower panel shows the captures for the year 2003. The size of the coloured circle represents the number of captures for specific individuals (see legend). Grey border surrounding clusters of circles indicates that the captures are in the same location.

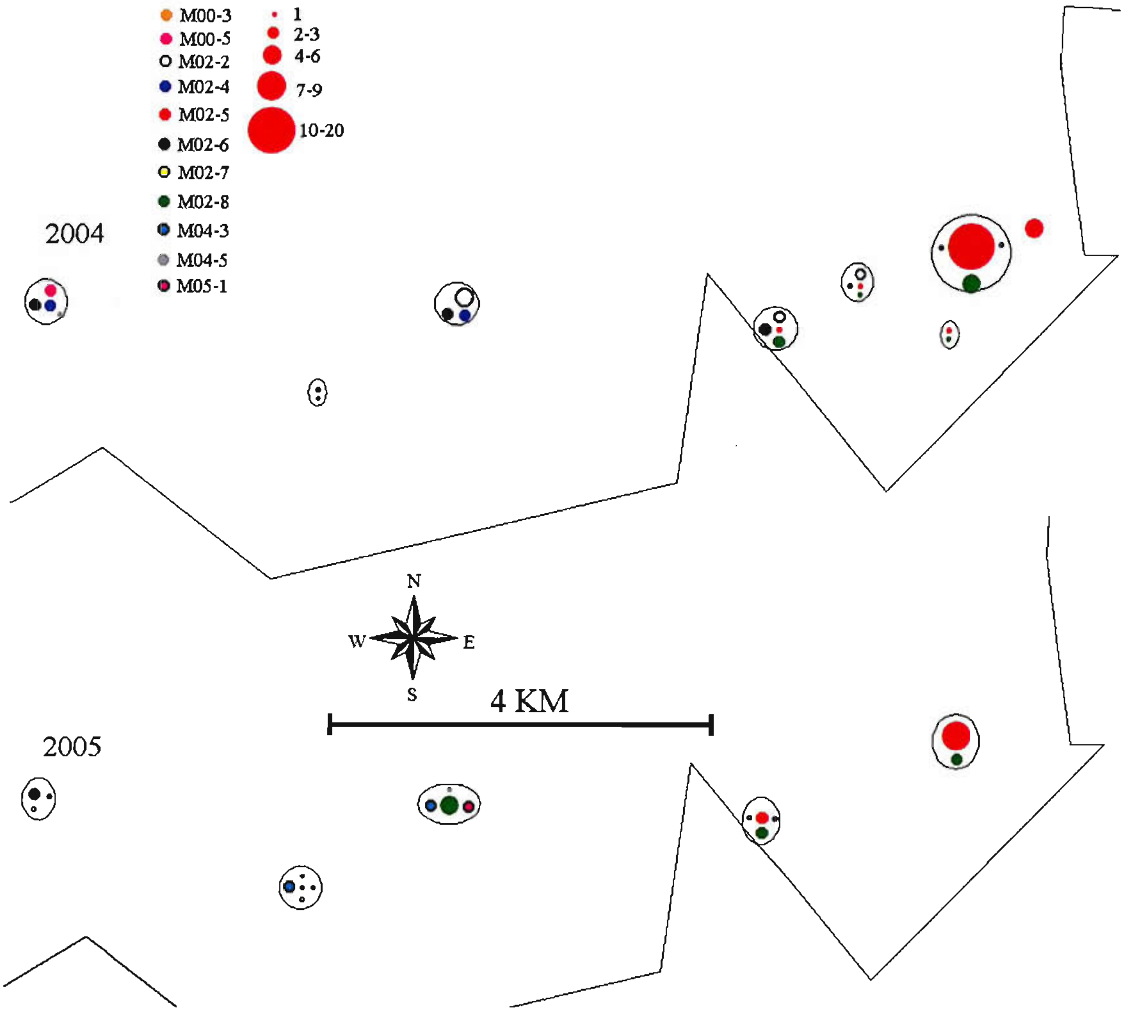

Figure B.4 Male jaguar captures in the south east region of the CBWS. The upper panel shows the captures for the year 2004 and the lower panel shows the captures for the year 2005. The size of the coloured circle represents the number of captures for specific individuals (see legend). Grey border surrounding clusters of circles indicates that the captures are in the same location.

# Appendix C

# Prey availability in the Cockscomb Basin, Belize

Table C.1 Mammals in Central American (from Reid 1991). Solitary individuals are given a 1 in group size, short notations of habitat and abundance are: ever=evergreen forest, dec= deciduous forest, var=variaty, var dry=variaty of dry habitats, var water= variaty of habitats having water, var forest= variaty of forest, sec= secondary forest, semi= semideciduous forest , brush=short brush habitat, unc=uncommon, ever water= evergreen forest near water, ever edges= evergreen forest near edges; in abundance column: rar=rare, com=common, abu=abundant. For forest with no human hunting.

| Weight range | | Genus | Species | Weight range(kg) | Group size | Habitat type | terrestrial or arboreal | General abundance |
|---|---|---|---|---|---|---|---|---|
| >10kg | * | Tapiridae | Baird's tapir (*Tapirus bairdii*) | 180.00 - 300.00 | 1 | dec/ever (water) | ter | rar/com |
| | | Cervidae | white tail deer (*Odocioleus virginianus*) | 25.00 - 43.00 | 1~4 | var (not ever) | ter | com |
| | * | Tayassuidae | white lipped peccary (*Dicotyles pecari*) | 27.00 - 40.00 | 20~200 | ever | ter | rar/com |
| | * | Cervidae | red brocket deer (*Mazama americana*) | 12.00 - 32.00 | 1 | ever | ter | com |
| | * | Tayassuidae | collared peccary (*Tayassu tajacu*) | 12.00 - 26.00 | 2~15 | var | ter | com |
| | * | Felidae | ocelot (*Leopardus pardalis*) | 7.00 - 14.50 | 1 | var forest | ter | rar |
| | * | Rodentia | Paca (*Agouti paca*) | 5.00 - 12.00 | 1 | var | ter | com |
| 5-10kg | * | Mustelidae | neotropical river otter (*Lutra longicaudis*) | 5.00 - 9.50 | 1~3 | undisturbed river | ter | rar |
| | | Cebidae | Central American spider monkey (*Ateles geoffroyi*) | 5.00 - 9.00 | 15~40 | ever | arb | rar |
| | * | Felidae | jaguarundi (*Felis yaguarondi*) | 4.00 - 9.00 | 1 | var | ter | rar |
| | * | Myrmecophagidae | northern tamandua (*Tamandua mexicana*) | 3.80 - 8.50 | 1 | var | both | com |
| | * | Cebidae | Yucatan black howler (*Alouatta pigra*) | 5.70 - 8.00 | 2~6 | ever/semi/sec | arb | com |
| | * | Procyonidae | northern raccoon (*Procyon lotor*) | 3.30 - 7.80 | 1 | var | both | com |
| | * | Dasypodidae | nine banded armadillo (*Dasypus novemcinctus*) | 3.00 - 7.00 | 1 | var dry | ter | abu |
| | * | Procyonidae | white nosed coati (*Nasua narica*) | 2.70 - 6.50 | 4~65 | var | both | com |
| | * | Mustelidae | tayra (*Eira barbara*) | 3.00 - 6.00 | 1~4 | var forest | both | com |
| | * | Felidae | margay (*Leopardus wiedii*) | 2.60 - 5.00 | 1 | var forest | both | rar |
| < 5kg | * | Procyonidae | kinkajou (*Potos flavus*) | 2.00 - 4.60 | 1~4 | var forest | arb | com |
| | * | Rodentia | agouti (*Dasyprocta spec.*) | 3.00 - 4.00 | 1 | var | ter | com |
| | * | Mustelidae | common hog-nosed skunk (*Conepatus mesoleucus*) | 1.50 - 4.00 | 1 | var dry | ter | com |
| | | Dasypodidae | northern naked-tailed armadillo (*Cabassous centralis*) | 2.50 - 3.50 | 1 | var | ter | rar |
| | * | Canidae | gray fox (*Urocyon cinereoargenteus*) | 1.80 - 3.50 | 1~4 | var (unc. ever) | both | com |
| | * | Mustelidae | striped hog-nosed skunk (*Conepatus semistriatus*) | 1.40 - 3.50 | 1 | ever | ter | com |
| | * | Mustelidae | greater grison (*Galictis vittata*) | 1.50 - 3.20 | 1~2 | ever | ter | rar |
| | * | Erthizontidae | Mexican porcupine (*Coenou mexicanus*) | 1.40 - 2.60 | 1 | var forest | arb | com |
| | * | Didelphidae | Virginia opossum (*Didelphis virginiana*) | 1.10 - 2.50 | 1 | var (unc. ever) | both | abu |
| | * | Didelphidae | common opossum (*Didelphis marsupialis*) | 0.60 - 2.40 | 1 | var | both | abu |
| | | Mustelidae | hooded skunk (*Mephitis macoura*) | 0.40 - 2.00 | 1~3 | dec/brush | ter | com |
| | | Procyonidae | cacomistle (*Bassariscus sumichrasti*) | 0.60 - 1.60 | 1 | var forest | arb | rar |
| | * | Didelphidae | gray four-eyed opossum (*Philander opossum*) | 0.30 - 1.40 | 1 | var | both | com |
| | | Leporidae | forest rabbit (*Sylvilagus brasiliensis*) | 0.70 - 1.30 | 1 | ever edges | ter | com |

# Appendix D

# Data tables

Table D.1 Sex of individual jaguars photographed during the study period (2002-2005).

| | **main surveys** | | | | | **Concentrated surveys** | | | | | **Line survey** | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **sex** | **2002** | **2003** | **2004** | **2005** | **2003(wet)** | **acc.** | **ant.** | **Juan.** | **Mex.** | **Wari.** | **Mitch.** | **6K line** |
| **Males** | 11 | 8 | 13 | 15 | 8 | 4 | 4 | 5 | 4 | 3 | 1 | 5 |
| **Females** | 0 | 1 | 4 | 4 | 2 | 2 | 3 | 1 | 0 | 2 | 1 | 1 |
| **Unknown** | 0 | 0 | 3 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |

Table D.2 The difference in total log10 male capture rate between camera locations with both male and female captures and camera locations with only males captures. Male capture rate is measured as total captures/100 camera days. Student *t*-test adjusted for unequal variance.

| | ***N*** | **Log10 Mean captures/100 days** | **Log10 s.e.** | **d.f.** | ***t*-value** | ***p*-value** |
|---|---|---|---|---|---|---|
| **Only males** | 47 | 0.59 | 0.057 | 50 | -2.73 | **0.01** |
| **Male and females** | 22 | 0.83 | 0.066 | | | |

Table D.3 Comparison of log10 maximum distance between camera captures of male and female individual jaguars. Student *t*-test adjusted for unequal variance.

| | ***N*** | **Log10 Mean(m)** | **Log10 s.e.** | **d.f.** | ***t*-value** | ***p*-value** |
|---|---|---|---|---|---|---|
| **Male distance** | 18 | 3.95 | 0.047 | 7 | 2.94 | **0.02** |
| **Female distance** | 6 | 3.65 | 0.090 | | | |

Table D.4 Comparison of log10 capture rate between male and female individual jaguars. Student *t*-test adjusted for unequal variance.

| | ***N*** | **Log10 Mean(capt)** | **Log10 s.e.** | **d.f.** | ***t*-value** | ***p*-value** |
|---|---|---|---|---|---|---|
| **Male Captures** | 22 | 1.16 | 0.130 | 20 | 2.82 | **0.01** |
| **Female Captures** | 10 | 0.59 | 0.150 | | | |

Table D.5 $\chi^2$test to compare proportion of the total number of jaguar male-male captures that were on the same day compared to the proportion of total number of male-female captures that were on the same day.

| | *N* (0 days) | *N* total | $X^2$ | d.f. | *p*-value |
|---|---|---|---|---|---|
| **Male-female** | 11 | 67 | 4.20 | 1 | **0.04** |
| **Male-male** | 18 | 248 | | | |

Table D.6 Student *t*-test adjusted for unequal variance to compare the time interval between male-female captures with the time interval between male-male captures for log10 transformed data.

| | *N* | Log10 Mean (days) | Log10 s.e. | d.f. | *t*-value | *p*-value |
|---|---|---|---|---|---|---|
| **Male-female** | 67 | 0.81 | 0.058 | 93 | -0.96 | 0.34 |
| **Male-male** | 248 | 0.87 | 0.026 | | | |

Table D.7 Students *t*-test adjusted for unequal variance to compare time interval between male-male captures and same male captures for log10 transformed data.

| Time between | *N* | Log10 Mean (days) | Log10 s.e. | d.f. | *t*-value | *p*-value |
|---|---|---|---|---|---|---|
| **Different jaguars** | 251 | 0.86 | 0.024 | 318 | -1.63 | **0.05** |
| **Same jaguar** | 151 | 0.94 | 0.031 | | | |

Table D.8 The number of runs of consecutive same male captures (observed), compared with the expected number of runs if the distribution of captures was random. *K* was the value of the average run.

| | Number of runs | *K* | Captures > *K* | Captures < *K* | *p*-value |
|---|---|---|---|---|---|
| **observed** | 219 | 0.48 | 221 | 242 | 0.23 |
| **expected** | 232.02 | | | | |

Table D.9 Total captures of puma and jaguars for 13 different surveys in CBWS between 2003 and 2005.

| survey | jaguar | puma |
|---|---|---|
| main2005 | 129 | 72 |
| main2004 | 100 | 86 |
| access | 99 | 35 |
| main2003(aut) | 72 | 78 |
| main2003 | 59 | 69 |
| JuanBr2004 | 29 | 48 |
| wari extension | 28 | 31 |
| antelope2004 | 26 | 11 |
| scrape2003 | 24 | 62 |
| 6Kline | 18 | 21 |
| mexican | 13 | 31 |
| mid trail | 12 | 7 |
| mitch trail | 10 | 25 |
| total | 619 | 576 |

Table D.10 The number of clusters (runs) of jaguar captures and puma captures through time for all the camera locations combined (observed), compared with the expected number of runs if the distribution of individuals was random. *K* is the value of the average run (*K* = 0.52).

|  | Number of runs | *K* | Captures > *K* | Captures < *K* | *p*-value |
|---|---|---|---|---|---|
| **observed** | 373 | 0.52 | 446 | 407 | **<0.01** |
| **expected** | 426.61 |  |  |  |  |

Table D.11 Comparison of trail use by jaguars and pumas using *t*-test adjusted for unequal variance. Upper panel: difference between puma and jaguars in the log10 number of cameras triggered along a single trail by single individual on a single day. Lower panel: the difference between puma and jaguars in the log10 number of cameras that were omitted during the walk along the trail.

| Number of cameras | *N* | Log10 Mean | Log10 s.e. | d.f. | *t*-value | *p*-value |
|---|---|---|---|---|---|---|
| Jaguar | 44 | 0.51 | 0.009 | 110 | -2.65 | **<0.01** |
| Puma | 70 | 0.55 | 0.014 |  |  |  |
| **missing captures** |  |  |  |  |  |  |
| Jaguar | 44 | 0.08 | 0.023 | 56 | 2.79 | **<0.01** |
| Puma | 70 | 0.02 | 0.009 |  |  |  |

Table D.12 Students paired *t*-test of the difference between the log10 capture rate of jaguars at each camera location when WL peccaries were present and when they were not present. Presence of WL peccaries was defined as 5 days either side of capture date.

| **WL peccary present** | ***N*** | **Log10 Mean captures/100 days** | **Log10 s.e.** | ***t*-value** | ***p*-value** |
|---|---|---|---|---|---|
| Yes | 45 | 0.28 | 0.068 | -2.72 | **0.01** |
| No | 45 | 0.46 | 0.061 | | |

Table D.13 Students paired *t*-test of the difference between the log10 capture rate of pumas at each camera location when WL peccaries were present and when they were not present. Presence of peccaries was defined a period of 5 days added on either side of capture date.

| **WL peccary present** | ***N*** | **Log10 Mean captures/100 days** | **Log10 s.e.** | ***t*-value** | ***p*-value** |
|---|---|---|---|---|---|
| Yes | 45 | 0.52 | 0.080 | 1.22 | 0.23 |
| No | 45 | 0.44 | 0.058 | | |

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