Ecology and conservation of the jaguar (*Panthera onca*) in the Cerrado grasslands of central Brazil

Dissertation zur Erlangung des akademischen Grades des
Doktors der Naturwissenschaften (Dr. rer. nat.)

Eingereicht im Fachbereich Biologie, Chemie, Pharmazie
der Freien Universität Berlin

vorgelegt von
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aus Essen

Berlin, November 2010

Diese Dissertation wurde am Leibniz-Institut für Zoo- und Wildtierforschung Berlin im Zeitraum April 2007 bis November 2010 angefertigt und am Institut für Biologie der Freien Universität Berlin eingereicht.

1. Gutachter: Prof. Dr. Heribert Hofer
2. Gutachter: Prof. Dr. Silke Kipper

Disputation am: 19. Januar 2011

This dissertation is based on the following manuscripts:

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CHAPTER 1

General introduction and outline

Man eaters and problem animals – the challenge of conserving large carnivores

The growth of the human population and associated impacts such as habitat loss, hunting, and the spread of invasive species or pathogens have devastating effects on biodiversity and are cause of virtually all current and ongoing declines of mammal species (Cardillo et al., 2004). A recent assessment of the conservation status of the world's mammals (Schipper et al., 2008) showed that 25 % of all mammals worldwide are threatened with extinction. Of the remaining species, many have experienced substantial declines of their total world range and population. Indeed, for 50 % of those species where population trends are known, these are classified as decreasing (Schipper et al., 2008).

Extinction is not only driven by extrinsic factors, but may also be facilitated by biological traits (Cardillo et al., 2005). A high trophic level, low population density and a slow life history are all associated with a high extinction risk in declining species (Purvis et al., 2000; Cardillo et al., 2004). As a consequence, carnivores, particularly the large species, are among the most threatened mammals worldwide (Schipper et al., 2008).

Carnivores comprise 287 extant species in 123 genera belonging to 16 families (Wilson and Mittermeier, 2009). Among the terrestrial carnivores, large-bodied species belong to the Canidae, Felidae, Ursidae and Hyaenidae families. Populations of many large carnivore species have drastically declined over the last 200 years (e.g., Mills and Hofer, 1998). Owing to their demanding spatial requirements and consequently low population density, even large reserves are often too small to harbour viable populations of large carnivores (e.g., Grumbine, 1990). Furthermore, carnivores are mobile species and roam beyond reserve borders where they come in contact with humans. Their predatory behaviour, both on wild and domestic animals, and sometimes humans, predisposes them to direct conflict with humans. As a consequence, large carnivores are often killed in retaliation against or to prevent attacks on livestock. Often, a perceived rather than actual danger posed by carnivores is sufficient to trigger their persecution (Treves and Karanth, 2003). Even inside reserves, death from anthropogenic sources is the most important threat to large carnivore populations because of edge effects, as mobile carnivores continue to be in conflict with people beyond reserve borders (Woodroffe and Ginsberg, 1998; Balme et al., 2009). Furthermore, where carnivores coexist with rural human populations, poaching can deplete their prey base and cause the decline or extinction of local carnivore populations (Karanth and Stith, 1999; Robinson and Bennett, 2000).

All these aspects point to a strong anthropogenic influence on large carnivore conservation and human population density can be a predictor for disappearance of carnivore populations (Woodroffe, 2000). Both cultural differences in tolerance of carnivores (Karanth and Chellam, 2009) as well as government attitudes (Woodroffe, 2000) can influence the persistence of carnivore populations. Linnell et al. (2001) showed that adequate wildlife management can foster large carnivore persistence even in areas of higher human density. Consequently, successful conservation of carnivores requires a complex set of information about species–specific ecological demands, population status, existing human activities and their influence on carnivore populations, and attitudes towards and perception of carnivores by the local human population.

Science for conservation – the challenge of studying large carnivores

Owing to their low population densities, often nocturnal and cryptic behaviour and sometimes the danger they pose to human observers, many carnivores remain relatively little studied (Karanth and Chellam, 2009). Studies based on direct observations are impaired by these traits for many carnivore species (MacKay et al., 2008b). Capture-based techniques where individuals are trapped or tracked down and marked with a radio-transmitter and/or, more recently, a Global Positioning System (GPS) device have been applied widely (Millspaugh and Marzluff, 2001). Especially the latter equipment has the potential to yield high resolution data on the spatial behaviour of the study animal to answer questions about movements and habitat use, but also aspects of foraging and social behaviour (for examples for jaguars *Panthera onca*, see Cavalcanti and Gese, 2009, 2010). However, physical capture and chemical immobilisation involve risks to the captured individual as well as to the researchers (Furtado et al., 2008). Furthermore, the very same behavioural and ecological traits that render large carnivores hard to observe can make them quite a challenge to capture. Consequently, most radio-tracking studies have to rely on a small sample size.

Non-invasive methods generally allow sampling of larger parts of the population under study and are therefore often preferable for the investigation of carnivore ecology, behaviour and population status (MacKay et al., 2008b). Particularly studies based on faecal sample collection and camera trapping have recently received increasing attention. Faecal samples have long been known to contain a wealth of information on animal biology and ecology

(Kohn and Wayne, 1997). The importance of faeces-based studies has greatly increased with the advances in genetic techniques since the 1990s that allow researchers to identify species, sex and individuals from DNA extracted even from deteriorated faecal samples (Kohn et al., 1995; Kohn and Wayne, 1997). While dogs had been used before for several kinds of research and conservation purposes such as tracking and capturing of animals, the early 2000s marked the arrival of scat detector dogs (Smith et al., 2001). Using their keen sense of smell and a strong drive to work for a reward, these dogs are trained to actively search for scats from one or several species and ignore scats from non-target species. Not relying on visual detection, dogs have a much higher chance to find small or cryptic scats, thus increasing our ability to detect scats in the field (MacKay et al., 2008a), unless the species in question is likely to select conspicuous sites for the deposition of faeces such as the European red fox *Vulpes vulpes* (Hofer, 1986) or the Eurasian badger *Meles meles* (Roper, 2010). Camera traps are regular photographic cameras embedded in a sturdy housing that are remotely triggered by a heat and motion sensor (passive system) or by an animal breaking an active infrared beam (active system; Kelly and Holub, 2008). The use of camera traps in studies of carnivore ecology goes back to the 1920s but remained infrequent until the 1990s because of the cost, time and effort they required (Kays and Slauson, 2008). Over the past 15 years, equipment has become increasingly affordable, field proof and reliable, and suited to the particular requirements of scientific studies such as fast trigger time.

In analytical terms, one major issue important to carnivore field research – and equally applicable to the study of other organisms – is that of imperfect detection. We can rarely obtain a complete census of individuals, species or occupied sites when investigating abundance, species richness or distribution, respectively. Rather, our data generally consist of a fraction of the true number of individuals/species/occupied sites we actually observed. The issue of imperfect detection and the resulting bias in ecological parameter estimates has received much attention (e.g., Seber 1982, 1992). The development of models accounting for imperfect individual detection, such as capture-recapture models (Otis et al., 1978) or imperfect detection of species, such as occupancy models (MacKenzie et al., 2006), and their implementation in easily accessible computer programs such as MARK (White and Burnham, 1999) or PRESENCE (Hines et al., 2006) have greatly advanced the ability of field ecologists to make sound inferences based on field data (e.g., Karanth et al., 2006). These models can be developed as hierarchical models and thereby explicitly describe the observation process as conditional on an underlying ecological process (Royle and Dorazio, 2008). For example, detecting a certain species at a particular sample unit (the observation process) is conditional on the species' occurrence (the underlying ecological process). Hierarchical models are now widely used for statistical modelling in ecology (e.g., Gardner et al., 2010).

Despite such methodological advances both in terms of physical and statistical-analytical tools, many studies of carnivores are limited to small data sets. In areas with low population density of the target species, even large-scale efforts can yield only sample sizes that forbid the use of many standard statistical procedures. Even non-parametric methods, which are in principle better suited to cope with small sample sizes because they are not based on assumptions about the distribution of the data, are not entirely free of assumptions and often require a minimum sample size (Zar, 1998). In addition, "frequentist" statistics (the conventional, prevailing statistical paradigm usually taught in basic courses at universities, as opposed to "Bayesian" statistics) are based on the underlying concept of asymptotic inference, i.e., the estimate of a parameter approaches truth as sample size approaches infinity. Thus, frequentist methods are not readily applicable to small data sets. Bayesian approaches do not rely on asymptotic inference and therefore may be more suited for sparse data (McCarthy, 2007). Bayesian statistics are currently becoming more popular with ecologists, as user-friendly and free software such as WinBUGS (Gilks et al., 1994) has become available.

In summary, investigations of carnivore ecology, even when performed with elaborated and up-to-date field methods, will sometimes yield data that are not particularly well suited for standard statistical procedures. Rather, researchers have to adjust, expand and combine existing methods to fit their particular situation and needs in order to extract the appropriate information from data sets collected with a large logistical, temporal and financial effort. Bayesian statistics do not compensate for the small sample size of limited data sets but they do provide an adequate approach to analysing sparse data. The absence of asymptotic inference and the flexibility of hierarchical modelling in Bayesian statistics provide powerful analytical tools. The downside is the substantial conceptual challenge associated with understanding the underlying principles for an adequate application.

The jaguar – a case study

The jaguar (Linnaeus, 1758; Figure 1.1) is the largest felid on the two American subcontinents and the third–largest big cat. The species' distribution stretches from northern Argentina to Mexico (Zeller, 2007) and covers – at least partially – 19 countries. Occasional sightings of the species across the Mexican border in New Mexico and Arizona (MacCain and Childs, 2008) is what remains of its US distribution which originally covered large parts of the southern USA (Sanderson et al., 2002). The species has lost close to 50% of its geographical range over the last century (Sanderson et al., 2002; Zeller, 2007) and has gone extinct in two of its former range countries (El Salvador and Uruguay; Caso et al., 2008). Indeed, the jaguar is among the top 20 species worldwide which suffered the highest absolute contraction of their distribution range over the last 500 years (Morrison et al., 2007). It is classified by the IUCN as Near Threatened with declining population trends (IUCN, 2010). Causes for the species' decline are manifold and typical for a large carnivore: rapid, large-scale habitat conversion, owing to an expanding agricultural frontier, and increasing urbanisation of the growing central and south American nations has greatly reduced suitable areas for jaguars. Furthermore, in the major beef producing nations of the world, hunting to prevent livestock predation or in retaliation to such predation is a considerable problem (Caso et al., 2008).

Public attitude towards and perception of the species is ambiguous. For many indigenous tribes, the jaguar has a strong mythical connotation. In pre-Columbian America, the species was the most prominent symbol of power and strength (Benson, 1998). Similar to other large cats, it is generally admired for its beauty and power (Saunders, 1998). Even in areas where it is intensively hunted, the species is often seen as a symbol for the region (Santos et al., 2008). Simultaneously, the species is often also regarded as a pest because of predation on livestock (Conforti and Azevedo, 2003; Zimmermann et al., 2005) and feared as a threat to human lives. Quite different to lions *Panthera leo*, tigers *Panthera tigris*, leopards *Panthera pardus* (Guggisberg, 1975; McDougal, 1987; Bailey, 1993) or pumas *Puma concolor* (Beier, 1991), confirmed unprovoked attacks on humans are extremely rare.

Jaguars are wide-ranging, with individual home ranges covering up to 1,000 km^2 (Silveira, 2004), occur at low population densities, from under 1 to 9 individuals 100km^{-2} (Paviolo et al., 2008 and Silver et al., 2004, respectively), generally prefer dense habitats in proximity to water, and avoid anthropogenically changed areas (Silveira, 2004; Cullen, 2006). Despite its wide distribution and the concern for its conservation, it remained the least studied member of the genus *Panthera* until about a decade ago (JCF, unpublished data); today, there is still a considerably smaller amount of published information for jaguars than for tigers, lions and leopards (Brodie, 2009). The geographic distribution of jaguar studies is far from uniform; for example, one third of all ecology-related scientific publications on jaguars were conducted in the Pantanal (Cavalcanti et al., 2010), whereas for many areas within the species' range no scientific information is published at all. Very recently, a few range or country-wide assessments of aspects of jaguar ecology and conservation have emerged (Sanderson et al., 2002; Sollmann et al., 2008; Tôrres et al., 2008; Rabinowitz and Zeller, 2010). With the profound lack of information on the species in large parts of its distribution, these large-scale assessments cannot currently be complemented with suitable local information necessary for actual implementation of conservation actions in specific regions or habitats.

Context of the dissertation


Fig. 1.1: *Jaguar in the Pantanal of Mato Grosso state, Brazil; picture by Douglas B. Trent.*

With its 8,500,000 km², Brazil covers approximately 50 % of the current jaguar range (Zeller, 2007). It also holds 50 % of the Amazon basin, the major stronghold for the long-term survival of this species (Sanderson et al., 2002; Sollmann et al., 2008), and large parts of the Pantanal floodplains, thought to harbour the second largest continuous jaguar population worldwide (Sanderson et al., 2002). Throughout Brazil, jaguars are found in five of the country's six biomes and a variety of environmental settings, from the coastal Atlantic forest in the south through the seasonal flood plains of the Pantanal and Cerrado savannas of central Brazil to the semiarid Caatinga in the northeast and the Amazon rainforest in the north. Conservation status of the species differs among these regions (Sollmann et al., 2008): in spite of its rapid destruction, the Amazon rainforest with its large and often interconnected nature and indigenous reserves still holds large jaguar populations. Although 95 % of the Pantanal are in private hands, the main economic activity of the region is extensive cattle ranching on native pasture, which permitted jaguars to persist and locally attain high population densities (Soisalo and Cavalcanti, 2006). Contrary, in the Atlantic forest, the most threatened biome of Brazil of which only 7 % remain, the jaguar has been disappearing at approximately 1° of latitude per decade due to habitat loss, hunting and a disappearing prey base (Leite and Galvão, 2002; Mazzolli, 2008). Haag et al. (2010) present genetic evidence for population isolation. In the Caatinga, a poor rural population competes with the jaguar for its mammalian prey; the natural vegetation cover is extremely fragmented and protected only to a very small degree. Hardly anything is known about the jaguar in this environment (Silveira et al., 2009). The species is also very little studied in the central Brazilian grasslands, where large-scale agriculture and consequent habitat loss and fragmentation are the biggest threats to the persistence of the species (Silveira and Jácomo, 2002).

In this context, the present dissertation was designed as part of the jaguar research and long-term population monitoring program in the Cerrado run by the Brazilian non-government organization Jaguar Conservation Fund (JCF; in Portuguese: Instituto Onça-Pintada). Specifically, the study aims to provide baseline information on the population status and ecological demands of the jaguar in the region of the Emas National Park (ENP), the focal site for jaguar research in the Cerrado by JCF. This information allows an assessment of the species' conservation status and major threats to its persistence in the study region. Within a methodological context, the study applies and develops analytical procedures that are designed to extract the maximum amount of information from and are adequate for small samples. With the focus on applied (conservation-oriented) questions, this study can be seen as a model for the analysis of the sparse data sets that often result from large carnivore field studies.

Study site

The Cerrado, or Brazilian savanna, is the second largest biome of Brazil, covering 1,783,200 km² or 22 % of the country and is exceeded in area only by the Amazon rainforest. It ranges from eastern Bolivia and Paraguay at 23° S to the equatorial zone in the north and varies in altitude from 100 m above sea level in the west to 1,500 m on the central Brazilian plateau (Motta et al., 2002). The Cerrado is characterised by climatic conditions typical of the moister savannas of the world and consists of a variety of vegetation types, ranging from open grassland (the "campo limpo", Figure 1.2c), to forests such as the Cerradão (Oliveira-Filho and Ratter, 2002). Watercourses are often accompanied by grassy swamps lined with Buriti palms (*Mauritia flexuosa,* Figure 1.2d) or gallery forest. Since 1950, the Cerrado has rapidly been altered through cattle farming, rice, corn, and soy bean plantations (Figure 1.2a). Today, up to 80 % of the Cerrado are considered degraded (Cavalcanti and Joly, 2002). Classified as one of the earth's 25 ecological hotspots (Myers et al., 2000), it is home to 20 carnivore

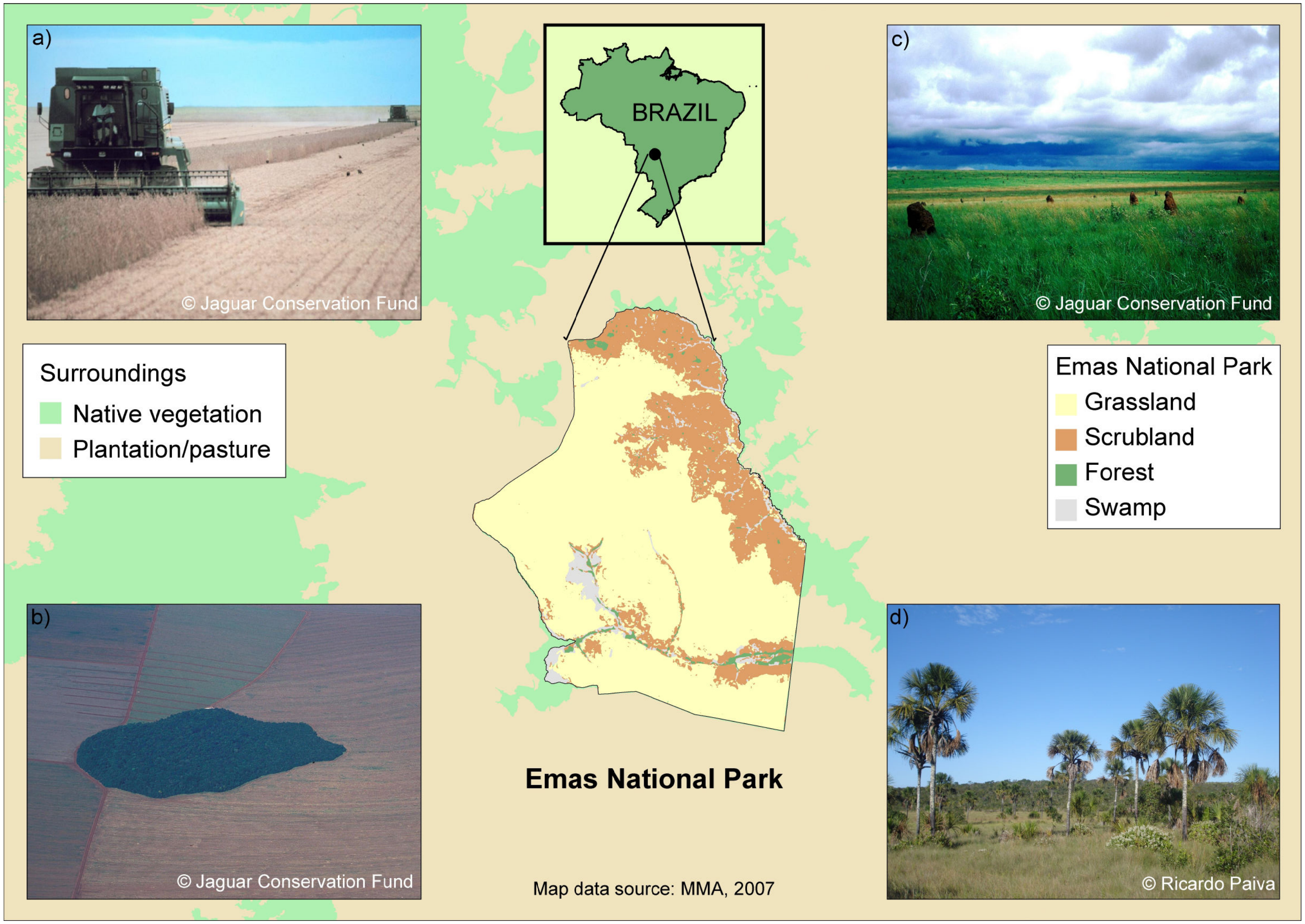

Fig. 1.2: *Emas National Park is situated in a region dominated by large scale agriculture (a) with small remaining habitat fragments (b); the park itself is mainly composed of grassland (c); buriti swamps (d) line the park's watercourses.*

species, out of which 10, including the jaguar, are listed as threatened on the Brazilian List of Species Threatened with Extinction (Marinho-Filho et al., 2002). Only 1.6 % of the biome is covered by federal or state reserves (Cavalcanti and Joly, 2002).

Emas National Park (Figure 1.2), with its area of 1,320 km², is one of Brazil's most representative Cerrado reserves. It is situated in the southwest of Goiás state, central Brazil, one of the most productive agricultural areas of Brazil (Klink and Moreira, 2002). The park was created in 1961, just before the southwest of Goiás was overrun by crop plantations. Open grassland (Figure 1.2c) contributes 97 % to the park area; the remainder is covered by gallery forest, marshes and Cerrado *sensu strictu* – shrub fields (Jacomo et al., 2004). The park hosts at least 13 endangered mammal species (Rodrigues et al., 2002). Holding one of the last protected jaguar populations of the Cerrado and the only protected jaguar population in the southwest of the biome, the ENP is of particular importance to regional jaguar conservation.

With the arrival of soybean in the early 1970s, most of the region was converted from extensive cattle farming on native pasture to soybean plantations (Jacomo et al., 2004, Figure 2a). With increasing demand for agrofuel (often misnamed as biofuel), the region is currently undergoing another major land use change towards sugar cane plantations. Approximately half of the surrounding area of ENP still consists of fragments of natural vegetation (JCF, unpublished data, Figure 1.2b). Fragments are mostly covered by Legal Reserves (LR) and Areas of Permanent Protection (APP), mandatory reserves that private landowners have to establish and maintain on their properties by law. LR consist of a certain proportion of the property's area – 20 % in the Cerrado – set aside for biodiversity conservation, whereas APP are buffer areas around watercourses or other fragile landscape features. This legislation creates a complex mosaic of vegetation with some potential to reconcile conservation with agricultural cultivation.

Structure of the dissertation

The results of the study are presented in the form of three manuscripts in chapters 2 to 4:

(1) Information on abundance and density delivers the most basic parameters necessary to assess a population's status (Lebreton et al., 1992). To assess the population status of the jaguar in ENP, in chapter 2 ("Improving density estimates for elusive carnivores: accounting for sex-specific detection and movements using spatial capture-recapture models for jaguars in central Brazil"), I analysed camera trapping survey data to estimate jaguar population

density. I applied both conventional non-spatial and novel, spatially explicit capture-recapture models to the data and discuss how model assumptions influence results.

(2) As the ecology of predators is influenced by the ecology of their prey (Karanth et al., 2010), investigation of the diet of large carnivores is of interest to conservation. In chapter 3 ("Prey selection and optimal foraging of a large predator: feeding ecology of the jaguar in central Brazil"), I investigated jaguar foraging ecology based on faeces collected with the help of scat detector dogs and confirmed to come from jaguars on the basis of molecular genetic techniques. In spite of the large-scale multi-year effort, the field study rendered a sample of faeces too small to apply standard statistical procedures. Therefore, I developed a rank-based optimal foraging model to investigate whether the jaguar exhibits opportunistic or selective foraging behaviour.

(3) Jaguars and pumas occur sympatrically throughout most of the jaguar's range. Partitioning of resources has been proposed as an important mechanism to facilitate the co-existence of ecologically similar species (Schoener, 1974) such as these two large cats. In chapter 4 ("Using hierarchical Bayesian modelling of site occupancy under imperfect detection to investigate resource partitioning between two sympatric large predators, the jaguar and puma in central Brazil") I investigated how these species partition space in ENP using hierarchical occupancy models that relate species occurrence to environmental variables and account for imperfect species detection.

Chapter 5 consists of a general discussion of the results of the dissertation. I focused the discussion on methodological considerations and possibilities for future methodological development, and the implications of my findings for local and Cerrado-wide jaguar conservation and research.

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CHAPTER 2

Improving density estimates for elusive carnivores: accounting for sex-specific detection and movements using spatial capture-recapture models for jaguars in central Brazil

Abstract

Owing to habitat conversion and conflict with humans, many carnivores are of conservation concern. Because of their elusive nature, camera trapping is a standard tool for studying carnivores. In many vertebrates, sex-specific differences in movements – and therefore detection by cameras – are likely. We used camera trapping data and spatially explicit sex-specific capture-recapture models to estimate jaguar density in Emas National Park in the central Brazilian Cerrado grassland, an ecological hotspot of international importance. Our spatially explicit model considered differences in movements and trap encounter rates between genders and the location of camera traps (on/off road). We compared results with estimates from a sex-specific non-spatial capture-recapture model. The spatial model estimated a density of 0.29 jaguars 100km^{-2} and showed that males moved larger distances and had higher trap encounter rates than females. Encounter rates with off-road traps were one tenth of those for on-road traps. In the non-spatial model, males had a higher capture probability than females; density was here estimated at 0.62 individuals 100km^{-2}. The non-spatial model likely overestimated density because it did not adequately account for animal movements. The spatial model probably underestimated density because it assumed a uniform distribution of jaguars within and outside the reserve. Overall, the spatial model is preferable because it explicitly considers animal movements and allows incorporating site-specific and individual covariates. With both methods, jaguar density was lower than reported from most other study sites. For rare species such as grassland jaguars, spatially explicit capture-recapture models present an important advance for informed conservation planning.

Key words: Bayesian analysis, camera trapping, density estimation, *Panthera onca*, sex-specific movements

Introduction

Owing to worldwide, large-scale habitat conversion and direct conflict with humans, many large and wide-ranging carnivores are of conservation concern. Although many charismatic species such as the big cats have received considerable attention through research over the past decade (Brodie, 2009), their populations continue to decrease (IUCN, 2010). Abundance and population density are key baseline parameters for conservation planning (Lebreton et al., 1992; Reid et al., 2002). Yet, reliable estimates are hard to obtain for these species because of their elusive nature and the spatial and temporal scale of their movements that need to be addressed by conservation-oriented studies (Karanth et al., 2006; Karanth and Chellam, 2009).

Camera traps have considerably advanced our ability to study elusive animals (Kays and Slauson, 2008). They have the advantage of being non-intrusive and applicable over large areas with relatively moderate effort (Silveira et al., 2003). Today, camera trapping is used to study a variety of aspects of wildlife ecology, ranging from species presence (e.g., Linkie et al., 2007) or behaviour (e.g., Harmsen et al., 2009) to relative abundance within a species assembly (e.g., O'Brien et al., 2003). Particularly for species with individually identifiable coat patterns, data from camera trapping can be analyzed within the analytically sound framework of capture-recapture models to estimate population abundance and density (Otis et al., 1978; White at al., 1981; Karanth, 1995; Karanth and Nichols, 1998) or population dynamics (Karanth et al., 2006; Gardner et al., in press). This methodology has been applied to several different species (e.g., maned wolves *Chrysocyon brachyurus* - Trolle et al., 2007, pumas *Puma concolor* - Kelly et al., 2008, common genets *Genetta genetta* - Sarmento et al., 2010) and is most commonly used to study individually distinctive large cats (e.g., Karanth and Nichols, 1998; Silver, 2004).

Though widespread, the use of camera trapping in combination with capture-recapture models has an important shortcoming that it shares with other methods applied to estimate abundance: the interpretation of abundance, or specifically the estimation of the area this abundance refers to (e.g., Karanth and Nichols, 1998; Royle et al., 2009). Whereas models assume geographic closure of the population, i.e., no movement on and off the sampling grid (White et al., 1982), this assumption is generally and widely violated (e.g., Karanth and Nichols, 1998), especially for large mammals. The standard approach is to buffer the grid with half the mean maximum linear distance moved by individuals captured in more than one trap (MMDM, Karanth and Nichols, 1998). Although this approach performed well in simulation studies (Wilson and Anderson, 1985), it is an ad hoc approach with little theoretical justification (Williams et al., 2002). Other approaches have been used to estimate buffer width, for example the full MMDM (twice the MMDM – fMMDM), or the radius of an average home range, both based on telemetry data (Soisalo and Cavalcanti, 2006) and on information from the literature (Wallace et al., 2003). Since density estimates are directly influenced by the chosen buffer width, comparison of estimates from different methodologies becomes difficult.

Spatially explicit capture-recapture (SECR) models are a recent advance in the field of density estimation (Efford, 2004; Royle and Young, 2008). These models make use of the spatial location of captures in order to first determine an individual's activity centre and then to estimate the density of activity centres across a precisely defined polygon containing the trap array (Gardner et al., 2009; Royle et al., 2009). They thereby circumvent the problem of estimating the effective area sampled. SECR models can be implemented within a Bayesian framework and therefore provide valid inferences even with small sample sizes. The 'pseudo-code' used by the freely available software WinBUGS (Gilks et al., 1994) provides an easy-to-use and flexible framework for fitting Bayesian SECR models.

The flexibility of these models also allows for the incorporation of other factors of interest, for example sex as an individual covariate (Gardner et al., 2010). Differences between the sexes in their behaviour and space use are typical for vertebrate social organizations and particularly most felids, where the home range or territory of a single male or a group of males may partially or completely overlap the generally smaller home ranges or territories of one to several females (Sandell, 1989). The resulting differences in space use and movement between the sexes will be reflected in differences in encounter probability of camera traps and should be taken into account when estimating population density and abundance.

The jaguar *Panthera onca* (Linnaeus, 1758) is the largest American felid and the third-largest big cat. It occurs from the south-western United States and Mexico to northern Argentina. Over the last century, the species' range has contracted to approximately 55 % of its original extent (Zeller, 2007) because of loss of natural habitat and persecution (Sanderson et al., 2002). The IUCN classifies the jaguar as Near Threatened (IUCN, 2010). In spite of its wide distribution and conservation concern, the species remains less studied than most other large cats (Brodie, 2009).

Here, we used SECR models to estimate jaguar abundance and density in Emas National Park (ENP), which holds one of the last jaguar populations in the Cerrado savanna of central Brazil. The Cerrado was identified as one of the earth's 25 ecological hotspots (Myers et al., 2000) and is threatened by rapid and large-scale habitat loss. The biome has been neglected by conservation oriented research and few studies have previously investigated jaguar ecology and conservation status in this biome. We therefore deployed 119 camera trap locations across the entire 1,320 km² of ENP - the largest single-site camera trapping study implemented for jaguars. Considering the sex-specific differences in behaviour outlined above, we incorporated into the SECR model sex-specific parameters and compared its results with those from a sex-specific but non-spatial approach. Our study not only provides novel information about jaguar ecology in the Cerrado but also has general implications for the modelling of population densities for most sampling designs for large carnivores and other elusive species.

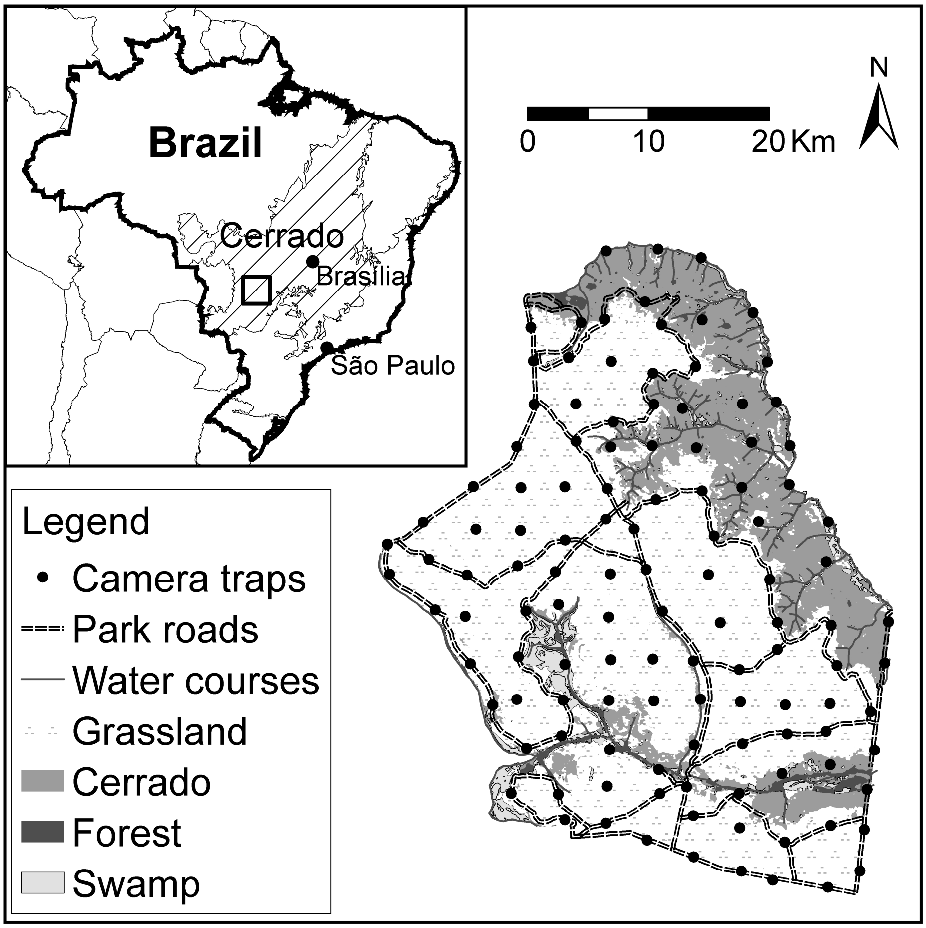

Fig. 2.1: *Location of Emas National Park in Brazil (square in inset) and map of the study area with camera trap locations (dots).*

Material and methods

Study area

Emas National Park, listed as a Human Heritage Reserve by UNESCO, is located in south-western Goiás state (18º 19'S, 52º 45'W; Fig. 2.1) in the Cerrado savanna of central Brazil. The park has a size of 1,320 km² and protects large tracts of grassland plains (97 %), small patches of shrub fields (1 %), marshes, and riparian forest (2 %). During the wet season (October to March), rainfall averages 1,500 mm. There is very little precipitation during the rest of the year, when daytime temperatures can reach 40° C and night temperatures may drop to -1.5° C (IBDF/FBCN, 1981). ENP is situated in a highly productive agricultural area. Large-scale soybean, corn and sugar cane plantations dominate and fragment the regional landscape. This situation is typical of the Cerrado: Brazil's second largest biome covers 21 % of the country's area but over the last 35 years more than half of it was transformed into cultivated land (Klink and Machado, 2005). Today, only 1.9 % is strictly protected and 80 % is considered degraded (Cavalcanti and Joly, 2002).

Camera trapping and data preparation

We deployed 119 camera trap stations on a park-wide 3.5 x 3.5 km grid (Figure 2.1). A maximum distance of 3.5 km between traps was recommended on the basis of the smallest jaguar home range recorded to date to ensure that all animals in the study area are exposed to traps and thus, in theory have a capture probability >0, a prerequisite for the non-spatial capture-recapture models (Karanth and Nichols, 1998; Silver, 2004). We adjusted the locations of the trap stations to maximize the number of traps along park roads for logistic reasons and to maximize capture probability (Karanth and Nichols, 1998, 2002). At off-road locations, we installed cameras along game trails. Each station consisted of two camera traps (the 35-mm LeafRiver C1-BU, Vibrashine Inc., Taylorsville, MS 3968, USA) facing each other with a lateral offset of approximately 30 cm to avoid flash interference. Camera traps were strapped to trees or stakes approximately 40-50 cm above ground, as recommended by Silver (2004).

Since cameras were easily triggered by sunlight in the predominantly open habitat of ENP, we programmed cameras to work throughout day and night in shady locations and only during the night in locations exposed to sunlight. For analyses, we only considered jaguar photographs taken at night. We installed camera traps in March 2008, kept them in the field for 85 consecutive days and checked them at 10-14-day intervals to replace film rolls and batteries.

We identified jaguar individuals in photographs based on their unique spot patterns and identified gender by secondary sexual traits. We divided our sample period into 17 5-day trapping occasions. For the non-spatial capture-recapture models we noted whether an individual had been photographed at all or not during each occasion (the binary encounter history of each individual). For the SECR approach, we noted how often an individual was photographed at each trap during each occasion (the count history of each individual).

Spatial model

SECR models are essentially generalized linear mixed models (GLMM) that assume an unobserved activity centre $\mathbf{s}_i$ for each individual i, which remains constant over the survey (the random effect). The encounter rate of an individual with a given trap is a monotonically decreasing function of the distance from the activity centre to that trap. y_{ij}, the number of times animal i is caught by trap j during a sampling occasion, is a random variable following a Poisson distribution,

$$y_{ij} \sim \text{Poisson}(\lambda_{ij})$$

Here, we model variation in λ_{ij} by allowing for sex-specific encounter rates and a sex-specific movement parameter σ. Assuming that the Poisson mean λ_{ij} decreases according to a normal probability density function,

$$\lambda_{ij} = \lambda_0 * \exp(-d_{ij}^2/\sigma^2),$$

the complete model in its log-linear form (Royle and Gardner, in press) is as follows:

$$\log(\lambda_{ij}) = \log(\lambda_0[k_i]) + \log(\rho[r_j]) - (1/\sigma^2[k_i]) * d_{ij}^2$$

Here, λ_0 is the baseline encounter rate, i.e., the expected number of captures of individual i at trap j during a sampling occasion when an individual's activity centre $\mathbf{s}_i$ is located precisely at trap j, and k is a binary vector that indicates the sex of individual i (i.e., $k_i = 1$ for males, 0 otherwise). ρ is a road effect where $\mathbf{r}$ is a binary vector that indicates whether trap j is on or off a road ($r_j = 1$ if the trap is located on a road, and 0 otherwise). Lastly, $d_{ij} = |\mathbf{x}_j-\mathbf{s}_i|$ is the distance from individual i's activity centre ($\mathbf{s}_i$) to trap j located at $\mathbf{x}_j$ ($\mathbf{x}_j$ being a pair of UTM latitude and longitude coordinates), and σ is the parameter that controls the shape of the distance function. We can translate σ into a 95 % home range radius by assuming a circular bivariate Normal model for movement.

Density (*D*) is a derived parameter that we calculate by dividing *N* by the area of *S*, where *N* is the number of activity centres in *S,* an arbitrarily large area that includes the trap polygon. We used a 40-km buffer from the outermost coordinates of the trapping grid, corresponding to an area *S* of 15,832 km².

Because *N*, the number of individuals is unknown, we used a Bayesian analysis by data augmentation of the model (Royle et al., 2007), which was implemented in the program WinBUGS (Gilks et al., 1994), accessed through the program R, version 2.10.1 (R Development Core Team, 2009) using the package R2WinBUGS (Sturtz et al., 2005). To do so, we let *M* be a number that is larger than the largest possible population size (i.e., the number of activity centres *N*) in *S*, and *n* be the number of detected individuals. We assume a prior distribution for *N* that is uniform over the interval (0, *M*) and augment the observed data set with an arbitrarily large number ($M - n$) of individuals whose photographic encounter histories are all 0. This reformulation of the model based on data augmentation is a zero-inflated binomial mixture and the number of activity centres *N* in *S* is then estimated as a fraction of *M*.

For model analysis, WinBUGS uses Gibbs sampling, a Markov chain Monte Carlo (MCMC) method simulating samples from the joint posterior distribution of the unknown quantities in a statistical model (Casella and George, 1992). MCMC chains are started at arbitrary parameter values and since successive iterations depend on the outcome of the previous iteration, the start value will be reflected in a number of initial iterations that should be discarded (the burn-in). This characteristic can also lead to autocorrelation of successive iterations. To avoid autocorrelation, a thinning rate is specified as every i^{th} iteration used in the characterization of the posterior distribution of the parameters. We ran three MCMC chains with 10,000 iterations, a burn-in of 5,000 and a thinning rate of three. This combination of values ensured an adequate number of iterations to characterize the posterior distributions, that MCMC chains showed no indications of autocorrelation or effects of the initial values, and that all chains converged (i.e. oscillated around essentially the same mean parameter value). We checked for chain convergence using the Gelman-Rubin statistic (Gelman et al., 2004), R-hat, which compares between and within chain variation. R-hat values below 1.1 indicate convergence (Gelman and Hill, 2006). Values for all estimated parameters were below 1.01. The WinBUGS code is available as supplementary material. The results below are presented as means ± standard errors of the mean (S.E.M.).

Non-spatial capture-recapture model

To estimate jaguar abundance N and sex-specific capture probability p under a non-spatial model, we used the full closed capture-recapture models in program MARK (White and Burnham, 1999). These models allow p to vary among groups of individuals, in our case between males and females, as well as with time or as a function of a behavioural response to trapping. The model with a sex-specific p had lower values of the Akaike Information Criterion adjusted for small sample size (AICc, Burnham and Anderson, 2002) than models with equal p for both sexes, a behavioural response in p or time variation in p. The AICc of the best model was at least 2 units lower than any other AICc, a difference sufficient to warrant a clear decision to prefer this model (Burnham and Anderson, 2002). Therefore, and because we are predominantly interested in a comparison with the spatial model with sex-specific parameters, we do not present results from the other non-spatial models.

We used the MMDM to buffer the trap polygon (e.g., Karanth and Nichols, 1998; Silver et al., 2004). Large portions of the park's immediate surroundings are composed of crop plantations and cattle pasture (Fig. 2.1), habitat types generally avoided by jaguars in the study area (Silveira, 2004) and elsewhere (e.g., Cullen, 2006). We therefore subtracted unsuitable habitat from the buffer and added only area covered by native habitat to obtain the effective area sampled. We divided the non-spatial abundance estimate by the size of this area to obtain the final density estimate.

Results

We obtained 107 jaguar photographs of which 105 were taken at night. All pictures were suitable for individual identification and corresponded to 5 male and 5 female individuals. Photographic frequencies were heterogeneous among individuals and sexes: one male accounted for 42 of the records; only 15 pictures showed females.

For the SECR models, the posterior mean of male baseline encounter rate at a given camera λ_0 was 0.47 ± 0.48 photographs occasion^{-1} whereas for females λ_0 was 0.05 ± 0.02 photographs occasion^{-1}. The effect of off-road location (ρ) of a camera trap was 0.11 ± 0.04. The posterior mean number of activity centres in S was 46 ± 16, equivalent to a mean density of 0.29 ± 0.10 100km^{-2}. The posterior mean locations of the activity centres of the 10 observed individuals are shown in Figure 2.2. Sex ratio, expressed as the probability of being a male, was 0.18 ± 0.09. The posterior mean of σ for males was 22.10 ± 3.14 km and for females 6.18 ± 1.12 km. Further results of the posterior distributions of parameters are summarized in Table 2.1.

For the non-spatial model, the estimate of detection probability for males was 0.49 ± 0.05, and 0.09 ± 0.04 for females. Estimates of *N* were 5 ± 0.01 for males and 5.59 ± 1.61 for females. The MMDM was 15.40 ± 4.97 km for males and 4.47 ± 3.08 km for females. After removal of patches of anthropogenic habitat unsuitable for jaguars, which accounted for approximately 50 % of the buffer zone surrounding ENP, the effective area sampled was 2,004 ± 788 km^2 for males and 1,498 ± 422 km^2 for females. Consequently, male density was 0.25 ± 0.10 100km^{-2} and female density was 0.37 ± 0.15 100km^{-2}. The combined density of adult jaguars was then 0.62 ± 0.18 100km^{-2}. For comparison, combined density was 0.51 ± 0.19 100km^{-2} without removal of the area deemed unsuitable from the buffer strip.

Table 2.1. *Summaries of posterior distributions of sex-specific parameters from spatially explicit capture-recapture models of jaguar camera trapping data from Emas National Park, central Brazil; σ = movement parameter [km], λ_0 = baseline encounter rate of on-road cameras [occasion^{-1}]; ρ = multiplicative coefficient for λ_0 at off-road locations; π = sex ratio, the probability of being a male; N = number of individuals in the 15,832 km² area containing the trapping grid; D = jaguar density [individuals 100km^{-2}].*

Parameter	**Units**	**Mean**	**SE**	**2.5 %**	**Median**	**97.5 %**
σ males	km	22.10	3.14	16.79	21.86	28.56
σ females	km	6.18	1.12	4.49	6.01	8.72
λ_0 males	Photographs occasion^{-1}	0.47	0.48	0.12	0.31	1.81
λ_0 females	Photographs occasion^{-1}	0.05	0.02	0.01	0.04	0.10
ρ	-	0.11	0.04	0.04	0.10	0.20
π	-	0.18	0.09	0.05	0.16	0.40
N	-	45.94	15.68	21.00	44.00	81.00
D	individuals 100km^{-2}	0.29	0.10	0.13	0.28	0.51

Discussion

Over the last decade, camera trapping in combination with capture-recapture modelling has become a standard tool in research on large felids. Spatially explicit capture-recapture (SECR) models are a recent development in this field and overcome the conceptual problem of interpreting abundance estimates from traditional non-spatial capture-recapture models (Efford, 2004; Royle and Young, 2008). Using this flexible class of models, we can also address other issues such as heterogeneity in capture rates owing to trap site-specific covariates (Kéry et al., in press) or individual covariates such as sex (Gardner et al., 2010).

Sex-specific and spatially explicit density models

Although most jaguar camera trapping studies observed a larger number of males than females, and generally, females are recaptured less often than males (e.g., Wallace et al., 2003; Silver et al., 2004; Salom-Pérez et al., 2006; Soisalo and Cavalcanti, 2006), this is the first study to quantify the difference between the sexes in detection rates and movements.

Female jaguars generally have smaller home ranges than males (Astete et al., 2008) and consequently, move less. They may also show a lower tendency to walk along roads and well established tracks (Salom-Pérez et al., 2007) where camera traps are preferably set up (Silver, 2004). Using the SECR approach permitted us to model these distinct movement patterns explicitly for both sexes, as this framework formalizes the relationship between exposure to the trap array and movements (Royle and Young, 2008; Gardner et al., 2009). The results corroborated what we expected on the basis of observations of previous jaguar camera trapping data and our own raw data: female baseline encounter rate at a given trap was close to one tenth of that for males. With an estimate just over 6 km, σ for females was close to four times smaller than for males. Consequently, the estimated sex ratio was extremely skewed towards females (about 1 male to 4 females). It is methodologically intuitive that the model interprets the low female encounter rate as an indication that there are many more females than we actually photographed. Although the skew initially seems remarkable in ecological terms, it reflects received and published wisdom on the distribution and overlap of male and female home ranges in large felids. For instance, Schaller and Crawshaw (1980) reported the presence of 2-3 female jaguars in the area of one male on a ranch in the Pantanal, and several authors reported male-female ratios of 1 to 3-4 for adult tigers *Panthera tigris* (Sunquist, 1981).

When using the non-spatial approach, female capture probability emerged as five times lower than male capture probability. However, this resulted in similar estimates of abundance for both sexes (5 males vs. 5.6 females). When we transform the count data into the binary format of detection/non-detection for non-spatial capture-recapture models and remove all of that spatial location data, much information about differences between the sexes is lost. The ability to use all data rather than a reduced binary set is an advantage of the SECR models, especially for the small data sets typical for studies of large carnivores.

The marked differences in estimated parameters provide insights into the distinct spatial behaviour of male and female jaguars. We showed that both sexes were photographed more often on than off road. However, when we compared λ_0 with estimates from a model without considering camera placement (on/off road), the increase in detection at on-road locations was greater for males than for females (results not shown). Thus, females apparently preferred roads less than males, without implying that females actually avoided roads as predicted by the hypothesis of Salom-Pérez et al. (2007). The overall encounter rate (SECR approach) or capture probability (non-spatial model) of females was much lower than that of males, probably owing to less frequent movements and much smaller home ranges. A model that accounts for such differences is more realistic and informative than a model that ignores them, and this approach can easily be extended to covariates other than sex by incorporating different facets of individual heterogeneity. These considerations are important for any species where males and females differ in their spatial behaviour, including all big felids, other carnivores such as bears (Gardner et al., 2010) and many other mammals.

Comparing the performance of jaguar density models

Density estimates under the spatial model (0.29 100km^{-2}) were about half of that under the non-spatial model. In the non-spatial model, we applied the MMDM algorithm, used by most jaguar camera trapping studies to estimate the effective area sampled (Maffei et al., 2004; Silver et al., 2004; Salom-Pérez et al., 2007; Paviolo et al., 2008). Estimates of the MMDM are constrained by the size of the sampling grid, as camera traps do not capture any movements beyond it. Thus, this approach likely underestimates movements and hence overestimates density. Even with the supposedly unsuitable habitat included in the buffer area, the combined density of 0.51 individuals 100km^{-2} was still much higher than under the spatial model. Combining camera trapping with GPS telemetry of jaguars, Soisalo and Cavalcanti (2006) could show that the MMDM algorithm underestimated movement and that the fMMDM was more realistic. Controversially, a similar study for leopards reached the opposite conclusion (Balme et al., 2009). These inconsistencies raise doubts about the usefulness of buffering approaches based on distance measures derived from the camera trapping grid.

In the present case, MMDM for both males (15.40 km) and females (4.47 km) were much lower than the SECR model estimates of home range radius (38.25 km for males and 10.69 km for females). If the MMDM is really used as a buffer, then this will result in an underestimate of the area effectively sampled and consequently inflate density estimates. This is an important issue and applies to virtually all camera trapping surveys which usually sample much smaller areas than the present study, and even for jaguars are limited to areas ranging from 90 (Salom-Pérez et al., 2007) to 550 km^2 (Soisalo and Cavalcanti, 2006).

On the other hand, it is possible that the spatial model may underestimate density. Within the framework of our current model, we assume that all 15,000 km² of *S* are homogeneous in terms of habitat suitability for jaguars, i.e., individuals are equally likely to live anywhere within this area. This is essentially the same assumption that the MMDM-based approach makes, buffering the trap array by some additional area to account for animal movements. In our study area, we know that habitat suitability does vary, since our sampling grid covered the ENP, a protected area, whereas the rest of *S* is fragmented and converted by about 50 % to cultivation, pastures and settlements (MMA, 2007). Subtracting such apparently unsuitable areas from the total buffer area, or from *S* (Royle et al., 2009) corrects for this heterogeneity but is an ad hoc approach and, thus to some extent, arbitrary. True jaguar density within the park is therefore likely underestimated by the spatial model and overestimated by the non-spatial models.

In contrast to our results, Silveira (2004) estimated jaguar density in ENP at an order of magnitude higher at 2 individuals $100km^{-2}$ for a region of 500 km² in the east of the park. Silveira (2004) considered this to be the only region of ENP inhabited by the species, therefore suggesting significant heterogeneity in habitat suitability for jaguars even within the park. Based on the spatial distribution of jaguar encounters in the present study (Figure 2.2), we draw the conclusion that jaguar movements are not nearly as restricted and, consequently, density across the entire park is hence much lower. With the increased amount of information on jaguar movements within ENP due to the large scale of the sampling grid and by explicitly modelling movements, the order of magnitude of our density estimates is likely to be more realistic for ENP as a whole.

Comparison of jaguar densities across the range

Jaguar density in ENP as estimated by this study is lower than most published estimates from across the species range. The population currently still residing in ENP is therefore more likely to go extinct in the medium to long term (Sollmann et al., 2008). At such low densities, most protected areas, when isolated by surrounding cultivated land as ENP, likely only harbour small populations. Much of central Brazil is covered by habitat considered to be very difficult for successful dispersal of jaguars (Rabinowitz and Zeller, 2010) and in areas with cattle ranching, conflict with humans because of livestock predation poses an additional threat to the species.

However, for ENP we also observed indications that the population is somewhat stable: some individuals had already been registered by camera traps in earlier years, occasional records of cubs and juveniles show that reproduction occurs, and sporadic camera trapping in 2009 showed the presence of new adult individuals in the population. The ability of a small population to persist is related to the potential reproductive output of a species, which is generally high for large felids (e.g., Lindzey et al., 1994; Karanth and Stith, 1999). Karanth and Stith (1999) showed that in a stochastic population model even small tiger populations had a low risk of extinction when simulated over 100 years. Thus, we may also expect some resilience to extinction in small jaguar populations.

There are some apparent trends in jaguar density: higher densities are encountered in tropical forests (up to 8.8 $100km^{-2}$ in Belize; Silver et al., 2004) and prey-rich seasonal flood plains of the Pantanal (6.7 $100km^{-2}$; Soisalo and Cavalcanti, 2006) than in drier habitats such as the Gran Chaco (2.3-5.4 $100km^{-2}$; Maffei et al., 2004) or the Caatinga (2.7 $100km^{-2}$; Silveira et al., 2009), or severely anthropogenically modified and degraded environments such as the Brazilian Atlantic forest (as low as 0.2 $100km^{-2}$; Paviolo et al., 2008). The present estimates fit into this overall pattern, coming from a severely anthropogenically modified drier region.

One has to bear in mind, however, that the density estimates from other studies do not use a spatially explicit Bayesian modelling technique and use some ad hoc rule of defining buffer zones. These non-spatial density estimates are directly influenced by the chosen width of the buffer (e.g., MMDM vs. fMMDM), making them difficult to compare. As our study shows, these buffer widths lead to a substantially smaller effective sampled area than the estimates of home range radius delivered by the Bayesian SECR models, thereby automatically inflating density estimates. Also, other factors such as the size of the effective area sampled (e.g., Smallwood, 1997; Gaston et al., 1999) can confound density estimates. For such purposes, SECR models have the additional advantage over the traditional approach in that they provide a unified and formalized approach to estimate density, thus rendering them comparable.

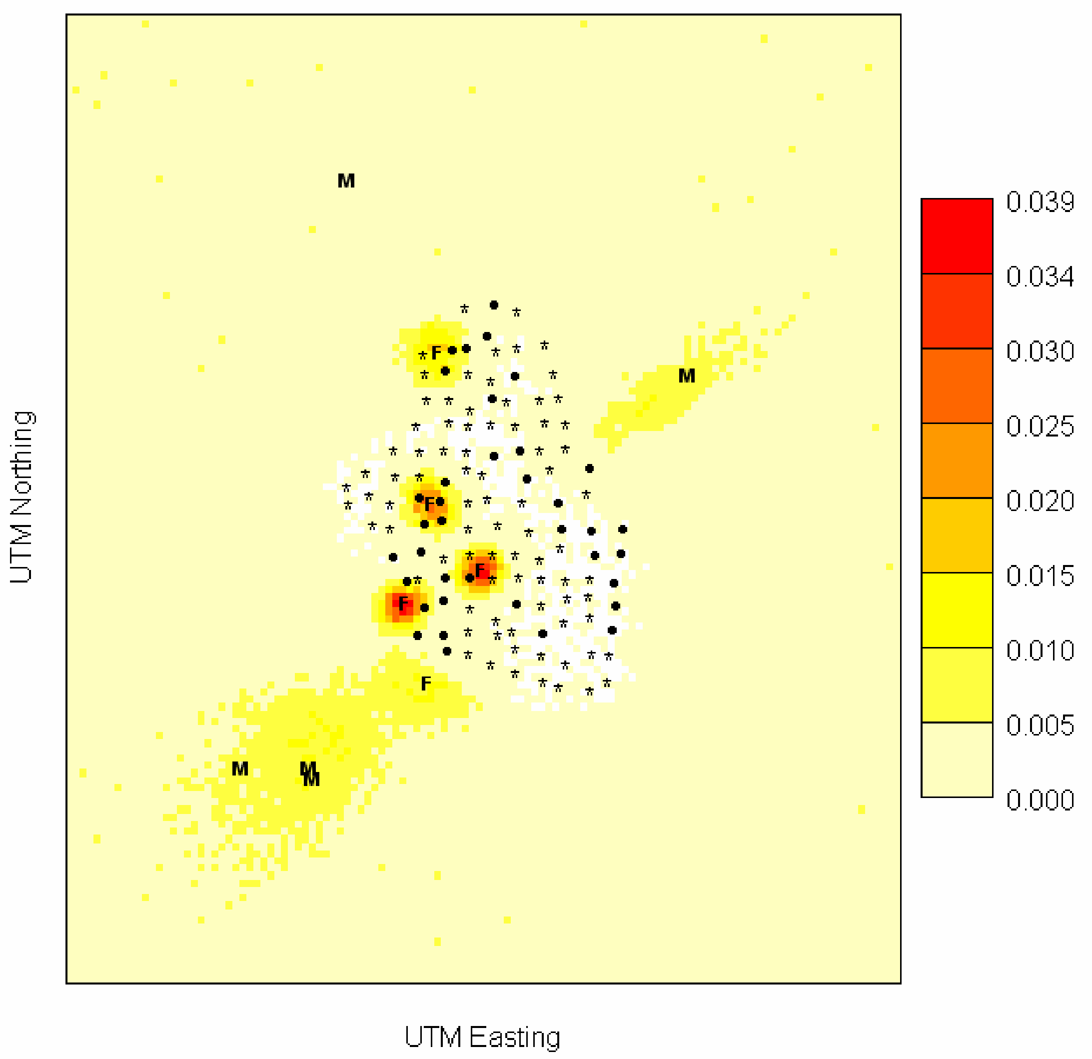

Fig. 2.2: *Map of posterior density of activity centres of jaguars in Emas National Park, central Brazil. Colours code for the estimated number of activity centres in each 1x1 km pixel; letters indicate mean activity centre location for identified individuals (M = males, F = females); asterisks indicate camera trap locations; dots indicate locations where jaguars were photographed.*

Future developments

While we believe that including sex as an individual covariate into both spatial and non-spatial capture-recapture studies is generally better than ignoring its obvious influence, we acknowledge the problem of sample size that becomes more severe with adding such covariates to a density model. Although for the SECR models the Bayesian framework provides valid inference for small sample size, this remains a problem. The standard errors of λ_0 and σ reported above show that there is still much residual variation in these parameters. While the model structure can easily be adjusted to account for individual heterogeneity in λ_0 and σ, in exploratory analyses (data not shown) our data set did not support the resulting number of parameters and some parameters became non-identifiable. Future work will have to identify whether this is purely an effect of small sample size or whether other properties of the data set are responsible for these difficulties.

We already discussed the consequences of the assumption of homogeneity of habitat suitability in the region S and the resulting underestimation of density for the study area. Furthermore, just as with buffer estimation in non-spatial density estimates, SECR models assume jaguar home ranges to be circular. For any situation where an animal is guided in its movements along specific landscape features, this assumption does not hold. In the present case, male jaguars followed the major water courses of the park (Figure 2.1), and their home range shape is better described as an ellipse. To reconcile the observed spatial pattern of captures with the assumption of circular home ranges, the model “places” the activity centres of males beyond the park border (Figure 2.2). Based on the actual habitat conditions in the park’s surrounding area, however, this is – in ecological terms – highly unlikely. Female home ranges are apparently much better described as circular. Relaxing the assumption on home range shape would be an interesting model development with the potential to benefit studies of many different species.

Conclusion

As for many populations of large cats, there is an urgent need to develop effective conservation strategies for jaguars in the Cerrado, as current conservation efforts are hampered by a persistent lack of knowledge. Occurring at generally low densities, big felids are not only particularly vulnerable to large-scale habitat loss, as it occurred in the Cerrado (Machado et al., 2004) and elsewhere, but despite improved methodologies and equipment they remain difficult to study. SECR models are an analytical step forward from traditional approaches to estimate densities of jaguars and other elusive species, since they overcome the problem of interpreting abundance and make use of the full information obtained by photographic data, including auxiliary spatial information. Nevertheless, these require large financial and logistical efforts in order to obtain sufficient data for reliable inference. Research and conservation efforts should therefore focus on the most pressing issues for the conservation of the species of interest. In the case of the Cerrado jaguar, this issue is where the remaining key populations are located and how a functional landscape connectivity can be created amongst them (Silveira and Jácomo, 2002). A first important step in this direction was undertaken by the effort of the Brazilian non-governmental organization Jaguar Conservation Fund to implement a dispersal corridor along the Araguaia River that starts in the immediate vicinity of ENP. It is a real priority that populations, such as the one studied here, avoid becoming isolated and thereby extinction-prone simply owing to stochastic factors that arise from their small size (Shaffer, 1981). The fact that the species has persisted in the ENP over the last decades despite somewhat adverse conditions suggests that the potential is there.

Acknowledgments

This study received financial support from the Disney Worldwide Conservation Fund, Fundação Monsanto, the Earthwatch Institute, the Memphis Zoo and the Leibniz Institute for Zoo and Wildlife Research. RS received a scholarship from the German Academic Exchange Service (DAAD). We thank ICMBio for granting permission to work in ENP and ENP management for logistical support. We are indebted to the entire Jaguar Conservation Fund team, all Earthwatch volunteers and interns, and especially Karlla Barbosa and Tiago Boscarato for their invaluable help with field work and picture analysis. Many thanks to J.A. Royle, J.D. Nichols and J. Hines for their help with data analysis.

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Supplementary material

WinBUGS pseudo-code for spatially explicit capture-recapture model with sex-specific movement and trap exposure

```
model {

lam0[1]~dgamma(.1,.1)  #priors for baseline trap encounter rates
lam0[2]~dgamma(.1,.1)

trap1~dunif(0,1)  #effect of off-road trap location on average trap exposure rate
trap[1]<-trap1
trap[2]<-1

psi~dunif(0, 1)  #probability of being in the sampled population
pi~dunif(0, 1)   #probability of being a male

sigma[1]~dunif(0, 25)  #priors for movement parameters
sigma2[1]<-sigma[1]*sigma[1]

sigma[2]~dunif(0, 25)
sigma2[2]<-sigma[2]*sigma[2]

for (i in 1:M){ #loop across zero-inflated data set

    z[i]~dbern(psi)
    SEX[i]~dbern(pi)
        SEX2[i]<-SEX[i] + 1
    SX[i]~dunif(xl, xu)
    SY[i]~dunif(yl, yu)

  for (j in 1:J) { #loop across all sampling sites

                D2[i,j] <- pow(SX[i]-trapmat[j,1], 2) + pow(SY[i]-trapmat[j,2],2)
                Eo[i,j] <- lam0[SEX2[i]]*trap[road[j]]*exp(-D2[i,j]/sigma2[SEX2[i]])
                log(pmean[i,j])<-log(T) + log(Eo[i,j])
                tmp[i,j]<-pmean[i,j]*z[i]
                y[i,j]~dpois(tmp[i,j])
                }

        }

N<-sum(z[1:M]) #number of individuals in polygon containing sampling grid

}
```

CHAPTER 3

Prey selection and optimal foraging of a large predator: feeding ecology of the jaguar in central Brazil

Abstract

Prey abundance is a predictor of carnivore density and prey depletion can threaten large felid persistence. Understanding prey selection is relevant to large felid conservation because it is usually unclear to what extent felids are dependent on specific prey species. Here we investigated jaguar *Panthera onca* feeding ecology in the Cerrado, central Brazil, based on a sample of genetically identified jaguar scats too small to perform the conventional quantitative comparison of prey consumed with prey abundance to investigate prey selection. We used distributional overlap between predator and prey derived from occupancy models as a measure of prey availability to investigate selectivity qualitatively. We further predicted prey preferences based on optimal foraging theory by ranking prey species in terms of net profitability based on expected foraging costs and energy gains. In 35 scat samples we observed at least eight prey species. We assessed availability and net profitability for the most important species – giant anteaters *Myrmecophaga tridactyla*, tapirs *Tapirus terrestris*, peccaries *Tayassu pecari* or *Pecari tajacu*, agoutis *Dasyprocta* sp. and opossums *Didelphis albiventris*. The giant anteater was predicted to be the most profitable prey, followed by tapirs, small mammals and finally peccaries. Giant anteaters contributed more than 75 % to the observed diet although distributional overlap with jaguars was lower than for tapirs and peccaries, indicating selection. Tapirs and peccaries contributed approximately 6 % to jaguar diet each, and small mammals contributed least to jaguar diet. In spite of some methodological drawbacks, the qualitative optimal foraging model predicted prey preferences well, only underestimating the role of peccaries. This shows that conclusions about jaguar diet were robust in spite of the small sample size. The study indicated that in ENP, selecting giant anteaters was the optimal foraging strategy for jaguars. This is the first study to systematically look into causes of prey selection in jaguars.

Key words: Bayesian statistics, camera trapping, Cerrado, diet, occupancy model, *Panthera onca*, ranking, small sample size

Introduction

One of the key questions in ecology is the functional link between species and their resources. The abundance of food resources has been shown to limit the density of consumers in many systems (Carbone and Pettorelli, 2009). For example in carnivores, prey abundance has been shown to be a good predictor of predator density (Carbone and Gittleman, 2002; Karanth et al., 2004). Populations of many carnivore species worldwide are of conservation concern because of habitat conversion and direct conflict with humans. Depletion of their prey base can reduce carnivore populations and lead to their local extinction (Karanth and Stith, 1999; Leite and Galvão, 2002; Karanth and Chellam, 2009). Thus, understanding dietary requirements of large predators is not only a step towards understanding an ecological system, but also a prerequisite for their conservation. Particularly for the Felidae, who are the most obligate meat eaters among carnivores (Kruuk, 1986), prey availability is an extremely important driver of ecology and consequently, an important issue in their conservation (Karanth et al., 2010).

Owing to their energy requirements, large felids rely on medium or large sized prey species and are unlikely to sustain themselves solely on small (<1kg) prey (Carbone et al., 1999; Macdonald et al., 2010). Within these limits (and some constraints posed by species-specific specialisations such as group hunting in lions *Panthera leo* or pursuit hunting in cheetahs *Acinonyx jubatus*), large felids are generally described as opportunistic hunters which can adapt to diverse prey spectra (Seymore, 1989; Karanth and Sunquist, 1995; Bertram, 1999; Iriarte, 1999; Hayward and Kerley, 2005; Hayward et al., 2006). Investigations of prey selectivity in felids were mostly based on selectivity indices that compare prey taken with prey availability and opportunism was defined as taking prey relative to its availability (e.g., Chesson, 1978; Manly, 2002). Most studies limit their assessment of prey availability to estimates or indices of relative prey abundance (e.g., Karanth and Sunquist, 1995; Novack et al., 2005; but see Cooper et al., 2007).

This concept of prey selection, however, does not explore the underlying reasons for selective foraging. Predators are thought to select prey that optimises their foraging, i.e., that maximises the amount of energy gained and minimises the amount of energy spent foraging (Griffith, 1975; Stephens and Krebs, 1986). Each prey species represents a particular set of foraging costs and benefit to the predator (Werner and Hall, 1974) and foraging costs are influenced by prey handling time, abundance and vulnerability (Schaller, 1972; Ware, 1973). The vulnerability of a prey is determined by its temporal and spatial distribution relative to the predator and predator avoidance and detection tactics such as crypsis or group living (Kruuk, 1986; Sunquist and Sunquist, 1989).

Consequently, a comprehensive investigation of feeding ecology requires sampling not only of the diet of a predator but also of a complex suite of aspects of predator and prey ecology, behaviour and population parameters, many of which may be difficult and costly to obtain. Predator diet itself may also be challenging to study because large felids and other large carnivores occur at low population densities. Consequently, researchers are often faced with small data sets, which complicate inferences about large carnivore ecology (Karanth and Chellam, 2009). As the hardest-to-study species are usually the ones we know least of, information contained in such small or incomplete data sets can still represent an important advance in our understanding of these species.

The jaguar *Panthera onca* (Linnaeus, 1758) is the largest cat of the American continent. With more than 80 prey species (Seymore, 1989), jaguars have been characterised as opportunistic predators that feed preferably on medium to large, primarily mammalian prey species, adapting their diet to local conditions (Lopez-Gonzales and Miller, 2002; Oliveira, 2002). The jaguar is classified as Near Threatened with decreasing population trends by the IUCN (IUCN, 2010). Its geographic range has suffered a contraction of approximately 45 % over the last century (Sanderson et al., 2002; Zeller, 2007) and prey depletion has been cited as one reason for diminishing or disappearing jaguar populations (Leite and Galvão, 2002). Owing to its cryptic habits, it remains less studied than most other larger cats, despite its wide distribution and conservation concern (Brodie, 2009).

While jaguar diet has been documented from several regions of the species' distribution, this is the first systematic investigation of jaguar feeding ecology in the Cerrado, one of the world's 25 ecological hotspots (Myers et al., 2000), where the species remains little studied despite a severe threat of large-scale habitat loss and fragmentation (Sollmann et al., 2008). With a small, skewed sample and a lack of quantitative data on prey availability we were unable to perform standard statistical procedures to test for prey selectivity. Instead, we use distributional overlap between each prey species and the jaguar as a proxy for availability to investigate prey selection. In a second step, in addition to distributional data we also use existing auxiliary information from field data and the scientific literature to develop a rank-based model of prey availability and vulnerability to predict prey preferences under optimal foraging theory. In addition to providing novel information on jaguar ecology in the Cerrado, this study demonstrates a novel approach to dealing with a small and incomplete set of information regarding predator feeding ecology.

Material and methods

Study area

Emas National Park, listed as a Human Heritage Reserve by UNESCO, is located in south-western Goiás state (18º 19'S, 52º 45'W; Figure 3.1) in the Cerrado savanna of central Brazil. The Park has a size of 1,320 km² and protects large tracts of grassland plains (97 %), small patches of shrub fields (1 %), marshes, and riparian forest (2 %). During the wet season (October to March), rainfall averages 1,500 mm. There is very little precipitation during the rest of the year, when daytime temperatures can reach 40° C and night temperatures may drop to -1.5° C (IBDF/FBCN, 1981). ENP is located within a highly productive agricultural area. Large-scale soybean, corn and sugar cane plantations dominate and fragment the regional landscape. This situation is typical of the Cerrado. Brazil's second largest biome covers 21 % of the country's area but over the last 35 years more than half of it was transformed into cultivated land (Klink and Machado, 2005). Today, only 1.9 % is strictly protected but 80 % is considered degraded (Cavalcanti and Joly, 2002).

Scat collection and identification

Between April and August 2009 we collected scats with the help of scat detector dogs. These dogs are trained to search for scats from specific species, in this study jaguar and puma *Puma concolor*. With their ability to detect small and cryptic scats that would otherwise go unnoticed, they increase efficiency of scat collection (Smith et al., 2001; Long et al., 2007). Dog-handler teams walked transects throughout ENP and along the eastern outside border with the aim to sample the entire population of at least 10 jaguars (Chapter 2). Visual species assignment of scats based on size and shape is error-prone, especially where similar-sized carnivores coexist (Kohn and Wayne, 1997; Taber et al., 1997), such as the jaguar and puma in ENP. Therefore, genetic species identification is recommended for any scat-based analysis (MacKay et al., 2008). The largest portion of each scat was stored frozen for dietary analysis. A small portion was stored in 96 % ethanol for subsequent genetic analysis. DNA was extracted based on the GuSCN/silica method and species identification was carried out with an optimised rapid classification protocol-PCR based on NADH5 mitochondrial DNA sequences as described in Roques et al. (2010). Additional scats confirmed by genetic techniques to be from jaguars from the same study area were provided by CV which she collected during several field seasons from 2004 to 2008. For a description of field and laboratory methods used by CV, see Vynne et al. (2010).

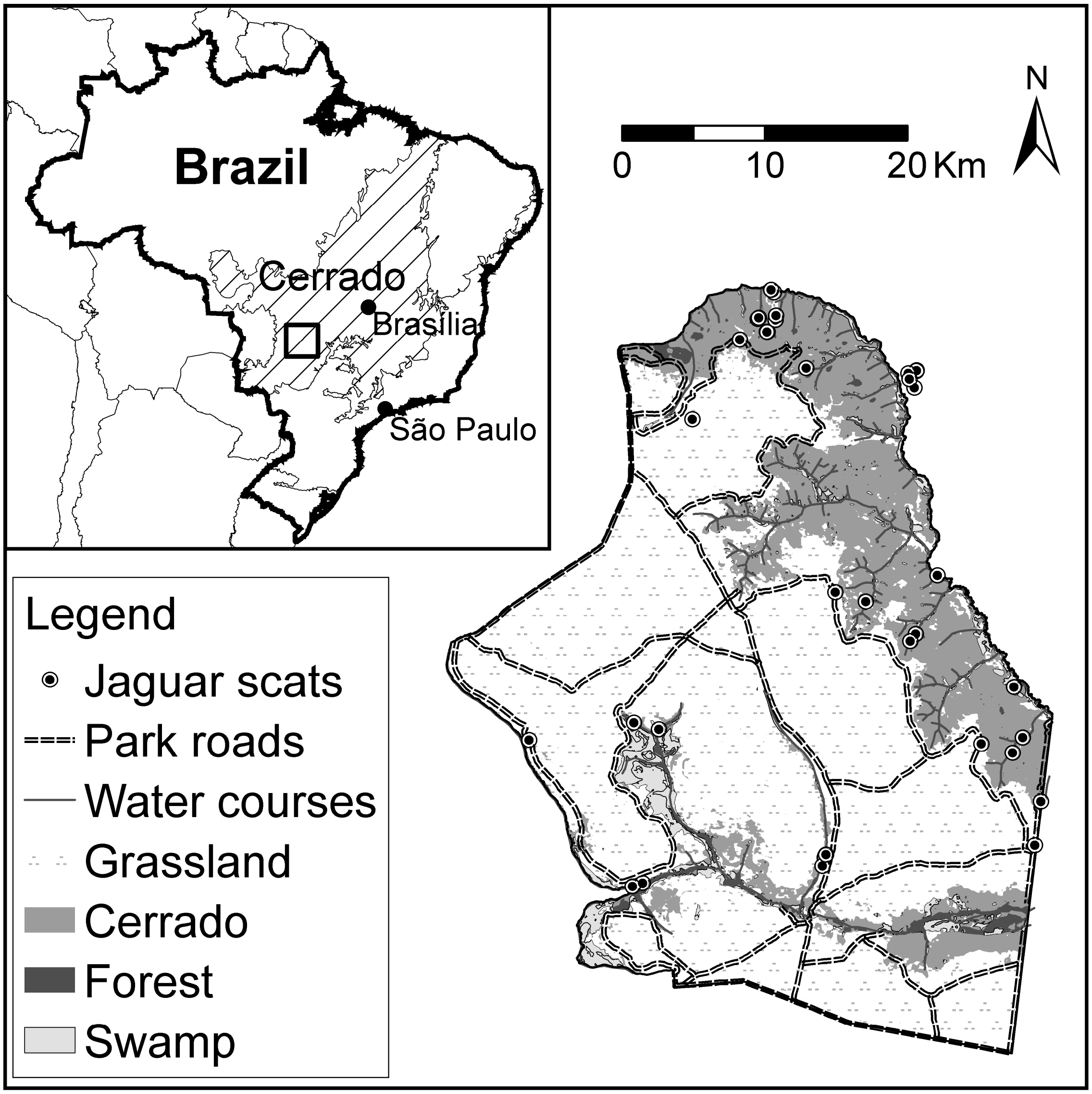

Fig. 3.1: Location of Emas National Park in Brazil (square in inset) and map of study site showing locations of scats detected with the help of scat detector dogs from 2004 to 2008 (Vynne et al., 2010), and in 2009.

Diet analysis

For diet analysis, we washed and dried scats and identified non-digested prey remains such as hairs, scales, nails, teeth and bone microscopically to the lowest possible taxonomic level using a reference collection (Hausman, 1920; Quadros, 2002). For each prey species *i* we counted the frequency of occurrence in the scats $\boldsymbol{f}$; when a scat sample contained remains of more than one species, these were counted as fractional contributions to the frequency of the respective species (Link and Karanth, 1994). We calculated relative scat frequency $\boldsymbol{fr}$ as

$$fr_i = f_i / \sum \boldsymbol{f}$$

Since our scat samples come from a total population of scats with unknown prey proportions, the set of prey frequencies can be viewed as a multinomial variable:

$$\boldsymbol{f} \sim \text{multinomial}(\boldsymbol{p}, N),$$

$\boldsymbol{p}$ being the vector of true category proportions of which $\boldsymbol{fr}$ is an estimate, and N being the total sample size. To assess uncertainty in $\boldsymbol{fr}$, we simulated 1,000 random draws from a multinomial distribution with $\boldsymbol{p} = \boldsymbol{fr}$ and calculated the mean and standard error (SE) of $\boldsymbol{p}$.

To correct for the actual contribution of biomass of each species to jaguar diet, we applied the method proposed by Wachter et al. (submitted) who, based on feeding trials with cheetahs, established a regression formula to calculate biomass consumed per field collectable scat as a function of live weight of prey species:

$$\boldsymbol{y} = 2.358 * (1\text{-}\exp(-0.075\boldsymbol{x})),$$

with $\boldsymbol{x}$ being mean prey body mass per feeding experiment and $\boldsymbol{y}$ being consumed prey mass per collectable scat. We calculated relative biomass consumed $\boldsymbol{b}$ as

$$b_i = p_i y_i / \sum \boldsymbol{py}$$

Given the lack of a specific regression for jaguars and the likely similar digestive system, we feel that this is a reasonable approximation. We obtained body weight of prey species from field data from ENP (JCF, unpublished data) and Reis et al. (2006). We assumed a normal distribution with coefficient of variation of 40 % for $\boldsymbol{y}$ (Link and Karanth, 1994), then simulated 1,000 random draws of $\boldsymbol{p}$ and $\boldsymbol{y}$ from their respective distributions and calculated the mean and SE of $\boldsymbol{b}$.

To evaluate the jaguar's dietary niche breadth, we calculated Levins' index B (Levins, 1968):

$$\text{B} = 1/\sum \boldsymbol{p}^2.$$

We standardized B according to Hurlbert (1978):

$$\text{B}_\text{A} = (\text{B}-1)/(I-1),$$

where B_A is Levins' standardised niche breadth and I is the total number of species in the diet. We calculated B_A for relative photographic frequency, $\boldsymbol{fr}$, and relative biomass consumed, $\boldsymbol{b}$, for each iteration of the simulation and report the mean B_A with SE.

Camera trapping

Between March and June 2008, we deployed 119 camera trap stations on a park-wide 3.5 x 3.5 km grid to estimate jaguar abundance and density in the study area (Chapter 2). Cameras were set along park roads and, at off-road locations, along game trails. Each station consisted of two camera traps of the 35-mm LeafRiver C1-BU type (Vibrashine Inc., Taylorsville, MS 3968, USA) facing each other with a lateral offset of approximately 30 cm to avoid flash interference. Camera traps were strapped to trees or stakes approximately 40-50 cm above ground. During the 3 months of sampling camera traps were checked at 10-14-day intervals for film roll and battery replacement. Since cameras were easily triggered by sunlight in the predominantly open habitat of ENP, we programmed cameras to work 24h/day in shady locations and only during night time in exposed locations.

Distributional overlap between predator and prey and prey selection

Energy spent searching for a particular prey is a continuous function of the time spent searching (Stephens and Krebs, 1986). It decreases with increasing encounter probability, which is influenced by prey abundance and spatial and temporal distribution in relation to the predator (Griffiths, 1975). As all prey species investigated here, as well as jaguars, were predominantly nocturnal-crepuscular (data not shown), we did not consider the temporal aspect further. Line transects are the usual method to determine prey abundance in predator diet studies (Cooper et al., 2007). The nocturnal, cryptic and wide ranging habit of the large mammals and the small size of small mammals make this method unfeasible for jaguar prey species in ENP. Likewise, individuals of prey species could not be individually identified so that capture-recapture models (Otis et al., 1978) based on photographic data were not an option. The widespread use of uncorrected indices based on photographic or other census count statistics is controversial since the true and unknown relationship between the index and actual abundance is unlikely to be constant across time, sites and species (Link and Sauer, 1998; Pollock et al., 2002). Therefore, we focused on the spatial distribution of prey in relation to the jaguar to assess availability.

We investigated the overlap in distribution between the jaguar and each prey species using camera trapping data and occupancy models (MacKenzie et al., 2006). These models can be formulated as hierarchical models describing the observation process and underlying ecological process separately (Royle and Dorazio, 2008). The true occupancy state O_i (0 or 1) of a sampling unit i is the outcome of a Bernoulli trial with probability of occupancy Ψ,

$$O_i \sim \text{Bernoulli}(\Psi).$$

Since non-detection of a species at a sampling unit can either be caused by true absence or by failure of detection, repeated visits to sampling units, x_i, are used to estimate detection probability p conditional on occupancy. The number of visits during which the species was detected at site i, y_i, is a random binomial variable with probability of detection p and number of trials x_i,

$$y_i \sim \text{Binomial}(p, x_i).$$

Using a logit link function on Ψ or p, both parameters can be modelled as linear functions of independent variables, as in regular logistic regression models (MacKenzie et al., 2006). We used distance to water course and percentage of dense habitat in the area sampled by the camera trap as independent variables on Ψ. We defined the area sampled by a trap as a 1,750-m buffer circle; this corresponds to half the average distance between neighbouring traps. As the spatial scale of our study is restricted and the study area is dominated by a grassland plateau, we believe that the watercourses and the cover that denser habitat types like the shrubby cerrado, the dry cerradão forest and the gallery forests provide, are the factors most likely influencing space use by the investigated species.

Owing to our sampling design and the mobility of the studied species, occupancy states are spatially correlated. To account for that, we defined the neighbourhood of each sampling site as all camera traps within a 7-km radius and added a random spatial effect to the linear predictor of logit($\boldsymbol{\Psi}$), with its value at site i, e_i, set as conditional on the value of $\boldsymbol{e}$ at all neighbouring sites, corresponding to a conditional autoregressive (CAR) model (Besag et al., 1991). This approach was sufficient to correct for spatial autocorrelation in occurrence of jaguars, the most mobile of the species investigated here (Chapter 4). We further used trap location on or off road as a categorical variable influencing p, as roads present clearer structures with better ability to "channel" animals towards camera trap stations than game trails.

We implemented the model using a state-space approach (Royle and Dorazio, 2008) where the latent occupancy state of each site, O_i, is explicitly estimated so that inference about the number of occupied sites can be made. This approach is particularly well-suited for situations where all or most of the sample units of interest are sampled, as in this case the probability of occurrence and the actual proportion of occupied sites can differ substantially (MacKenzie et al., 2006). Implementing a state-space model in a Bayesian manner is straight forward and allows the definition of functions of the estimated occupancy state (MacKenzie et al., 2006) and use of the free software WinBUGS (Gilks et al., 1994). By coupling each prey occupancy model with the jaguar model, this approach permits us to estimate the number of sampling sites occupied by both species, which we used to rank prey species according to their distributional overlap with the jaguar. We interpreted a departure of these ranks from the order of species observed in the diet as an indication of prey selectivity. A detailed model description, the WinBUGS code and further specifications are listed in the supplementary material I.

The optimal foraging model

To predict prey preferences under optimal foraging, we aimed to evaluate a set of the costs and benefits in terms of energetic expenditures and gains associated with foraging for prey species we identified in the jaguar's diet. We assumed that foraging costs arise from searching, detecting, hunting and handling a prey. As there are no direct data on costs of these activities for the jaguar, we ranked species based on characteristics that can be related to foraging costs and assessed using the available literature and field data. Whenever we used several characteristics for one aspect of foraging, we ranked species according to each characteristic separately, and established the overall rank based on the average of the partial ranks. This assumes that all investigated aspects contribute equally to overall foraging costs. While this may not be realistic, attributing different weights to the investigated aspects would entail a whole set of largely speculative assumptions. As ranks reflect costs, a high rank is associated with high foraging costs for the predator.

We assessed the following aspects of foraging (details about how we established ranks are listed in the supplementary material II):

1. *Search*: We evaluate costs associated with searching for a prey species based on overlap in distribution with the jaguar (as described above) and abundance. As elaborated above, our data were not suitable to estimate absolute abundance. Therefore, we used a corrected index based on camera trap data to rank prey species according to their abundance: We calculated the average number of photographs of a species at sites where it was found or estimated to co-occur with the jaguar. We only considered these sites, as we are interested in abundance as perceived by the jaguar, not throughout the study area. To correct for the fact that individuals of large mammals with home ranges that include several cameras contribute to the photo-count repeatedly, we estimated the average number of traps contained in an average home range and divided the total number of photographs by this number. We

evaluated the home range corrected photo-counts against species detection probability by camera traps to establish abundance ranks.

2. *Detection*: Once at a site where a prey species is present, the predator has to detect its prey. We ranked detectability assuming that groups are more easily detected than solitary individuals (e.g., Emmons, 1987; Crawshaw, 1995), larger animals are more easily detected than smaller ones (Ware, 1973), and species preferably encountered in open habitat are more easily detected than those preferring dense habitats. We based habitat preferences on the coefficients reflecting the influence of dense habitat on occupancy from the occupancy model described above.

3. *Probability of failed hunt*: A detected prey can still escape the predator. Hunting success is likely reflected in a predator's diet (Sunquist and Sunquist, 1989; Stander, 1991). We ranked the probability of failed hunts assuming that groups profit from increased vigilance and the confusion effect, thus having a larger chance to detect and avoid a predator (Pulliam, 1973; Lipetz and Beckoff, 1982), and that larger-bodied animals have a better chance of escaping a jaguar attack.

4. *Risk of injury*: Risk of injury is an important foraging cost, particularly for top predators (Berger-Tal et al., 2009). We ranked the risk of injury to a jaguar by assuming that large animals and groups pose a greater risk of injury (Sunquist and Sunquist, 1989), which is further enhanced by the presence of claws or tusks.

5. *Handling time*: Handling time is a key factor affecting foraging costs in optimal foraging models (Stephens and Krebs, 1986). We ranked handling time by assuming that it increases with increasing body size, as a jaguar may have to bring its prey to a suitable feeding spot or position. As no species observed in the diet had a carapace or shell, we did not consider physical characteristics of the prey species other than size.

Gross energy gain increases with prey size but reaches an asymptote at a size where predators are unable to consume the entire prey animal because of decay and loss to scavengers (Ackerman et al., 1986; Foster et al., 2009). We ranked the gross energy gain associated with a prey species based on species body mass, with all species ≥30 kg representing the same maximum gain. We calculated the difference of the foraging cost ranks and the gross energy gain ranks and then ranked species on their net profitability. We predicted that prey species should be consumed according to their profitability and compared predictions with the diet composition observed in scats.

Results

Jaguar diet

In 2009, two dog-handler teams walked 42 transects totalling 418 km. Fifty-six potential jaguar scats were detected by the dogs; an additional 11 scats were collected opportunistically during other activities in the field. Genetic identification of species was possible for 48 scats and 14 were identified as jaguar scats. CV provided an additional 25 genetically identified jaguar scats from 407 field surveys totalling 3,175 km (Vynne et al., 2010). Scats came from distinct areas within the park (Figure 3.1).

Table 3.1: *Prey species identified in 35 jaguar scats from Emas National Park, central Brazil. f: absolute scat frequency; p: average simulated relative scat frequency (standard error); MPW: mean prey weight according to unpublished data by the Jaguar Conservation Fund and Reis et al. (2006); BPS: biomass consumed per field collectable scat (BPS), following Wachter et al. (submitted); b: average simulated relative biomass consumed (standard error).*

Species	***f***	***p* (SE)**	**MPW (kg)**	**BPS (kg)**	***b* (SE)**
Tapir	2.00	0.06 (0.04)	239	2.36	0.08 (0.06)
Peccary	2.00	0.06 (0.04)	24.5	1.98	0.07 (0.05)
Giant anteater	26.17	0.74 (0.07)	30.5	2.12	0.76 (0.12)
Agouti	1.17	0.03 (0.03)	2.9	0.46	0.01 (0.01)
Opossum	0.33	0.01 (0.02)	1.25	0.21	<0.01 (<0.01)
Domestic cattle	1.00	0.03 (0.03)	175	–	0.05 (0.04)
Capybara	0.50	0.01 (0.02)	50	2.30	0.03 (0.03)
Unidentified felid*	1.33	0.04 (0.03)	–	–	–
Unidentified bird/reptile*	0.50	0.01 (0.02)	–	–	–

* *Not considered in calculations involving biomass because body weight could not be determined.*

Four scats did not contain identifiable prey remains. Of the other 35 scats, 29 contained remains of a single prey species, four contained remains of two species and two scats contained remains of three prey species. Giant anteater *Myrmecophaga tridactyla* was the most frequently encountered prey species and accounted for 74 ± 7 % of the total sample. We also found remains of tapir (*Tapirus terrestris*), capybara (*Hydrochaeris hydrochaeris*), opossum (*Didelphis albiventris*), domestic cattle (*Bos taurus*), white-lipped peccary (*Tayassu pecari*) and an unidentified peccary species (*T. pecari* or *Pecari tajacu*), an unidentified agouti species (*Dasyprocta* sp.), an unidentified bird or reptile, and unidentified felids (Table 3.1). Since the felid hair and the unidentified bird/reptile could not be identified to genus level, these were not considered in further analyses. We grouped scats with peccary remains, since for one sample the species of peccary could not be determined.

Giant anteaters contributed 76 ± 12 % to the consumed biomass; other species with a contribution above 5 % were tapir, peccary and cattle (Table 3.1). Niche breadth expressed as the standardised Levins' index was 0.104 ± 0.046 for scat frequencies and 0.121 ± 0.085 for relative biomass consumed.

Distributional overlap between jaguars and prey and prey selection

The only species for which we could perform occupancy modelling were the giant anteaters, tapirs, peccaries and the joint data set of agoutis and opossums, from hereon referred to as 'small mammals'. There were no photographic records of capybaras, as these semi-aquatic animals occur only on the limits of the park, or of cattle which only occur beyond the park border. Details on occupancy model results are listed in Table 3.2. In the occupancy model, we only considered covariates as having a strong influence on occupancy if their coefficient estimate had a 2.5-97.5 percentile of the posterior distribution – the Bayesian equivalent of a 95 % confidence interval, or BCI – that did not overlap 0.

Jaguar occurrence was positively correlated with increasing percentage of dense habitat and decreasing distance to water. The species occurred at 54 ± 4 % of all sample sites. Tapir occurrence was positively correlated with both habitat variables. This species had the largest distributional overlap with the jaguar (78 ± 3 % of jaguar occupied sites). For peccaries neither habitat variable had a strong influence on occurrence. Distribution overlap with the jaguar was 57 ± 7 %. For giant anteaters, occupancy increased with increasing distance to water and decreasing percentage of dense habitat; distributional overlap with the jaguar was 35 ± 3 %. Small mammal occupancy was negatively correlated with distance to water; they occurred at 18 ± 5 % of all jaguar occupied sites. The predicted prey preference of jaguars under the assumption of consuming prey relative to its availability as derived from the occupancy models were therefore tapir followed by peccary, giant anteater and small mammals. Compared with the observed diet composition, this indicates that jaguars selected giant anteaters, avoided tapirs and peccaries, and consumed small mammal according to their availability.

Table 3.2: *Factors influencing the distribution across habitats of jaguar and its prey species in Emas National Park. The occupancy model for the jaguar and its main prey species yielded coefficients (β) for distance to water (DIST) and percentage of dense habitat in a 1,750-m buffer (DENS); further, percentage of sites occupied (% Occ) and overlap with jaguar distribution in percent of jaguar occupied sites (% Olap); all values with standard error (SE).*

Species	***β*(*DIST*) (SE)**	***β*(*DENS*) (SE)**	**% Occ. (SE)**	**% Olap (SE)**
Jaguar	-1.46 (0.51)*	1.38 (0.80)*	53.90 (3.77)	/
Tapir	0.83 (0.51)*	1.13 (0.46)*	78.78 (2.59)	77.91 (3.33)
Peccary	0.23 (0.48)	-0.36 (0.34)	63.21 (6.09)	56.94 (7.27)
Giant anteater	0.83 (0.40)*	-2.02 (0.54)*	54.22 (2.12)	34.53 (3.37)
Agouti/Opossum	-1.88 (1.11)*	0.80 (0.47)	10.85 (2.81)	17.77 (4.73)

** parameter estimates whose 95 % BCI did not overlap with 0*

Table 3.3: *Foraging cost (in terms of ranks) for the main prey species of jaguar in Emas National Park associated with search, detection (D), probability of failed hunts (p(failed)), risk injury (Risk) and handling time (HT); with sum of all partial ranks (Sum), final foraging cost rank (FC), rank of gross energetic reward in case of a successful hunt (Reward), difference between reward and cost rank (Net gain) and resulting predicted preference rank (R).*

Species	**Search**	**D**	***p*(failed)**	**Risk**	**HT**	**Sum**	**FC**	**Reward**	**Net gain**	**R**
Tapir	1	3	3	3	4	14	3	3.5	0.5	3
Peccary	4	1	4	4	2.5	15.5	4	2	-2	1
Giant anteater	3	2	2	2	2.5	11.5	2	3.5	1.5	4
Agouti/ Opossum	2	4	1	1	1	9	1	1	0	2

Predicted prey preferences based on the optimal foraging model

For comparison, giant anteaters, tapirs, peccaries and the small mammals were also the only species considered in the optimal foraging ranking model. Individual ranks associated with searching, detection, risk of failed hunts, risk of injury for a certain prey type, the summary in terms of final foraging cost ranks and the related foraging benefit ranks are listed in Table 3.3 (and detailed explanations provided in the supplementary material II). Net energy gain as gross energy gain rank minus foraging cost rank was highest for giant anteaters, followed by tapirs, small mammals and peccaries. Following optimal foraging theory, jaguars should therefore prefer giant anteaters, followed by tapirs, small mammals and peccaries in this order. A comparison with the observed frequency or consumed biomass in the scats indicated that the optimal foraging model was a good predictor of prey preferences, only underestimating the importance of peccaries.

Discussion

Using readily available information, we investigated prey selection using distributional overlap with the predator as a proxy for prey availability, and ranked main prey species regarding their profitability to the jaguar based on criteria from optimal foraging theory. Optimal foraging model predictions coincided well with the observed preferences in a small set of scats – except for the underestimate of peccary –, providing support for the robustness of the results we obtained from this small sample. They explained selective tendencies observed when comparing prey availability to prey consumption.

Small sample size and lack of accurate auxiliary information such as prey abundance, distribution and vulnerability is a problem that applies to many studies of large carnivore foraging ecology. Scat collection is supposed to be inexpensive, relatively quick to apply and yield large sample sizes (Litvaitis, 2000). Yet, the present study yielded only 39 jaguar scats, in spite of a large-scale multi-year effort with scat detector dogs. Collection success was much higher for other target species: for example in 2009, 33 scats collected came from puma (also see Vynne et al., 2010). This is most likely a consequence of the low density of jaguars in the study area (Chapter 2). The spatial distribution of confirmed jaguar scats (Figure 3.1) suggests that most of the ENP jaguar population is potentially represented in our sample.

Jaguar diet in ENP

Jaguar diet in ENP consisted of at least eight mammalian species. Prey spectra reported for the jaguar from throughout its range are extremely variable, ranging from six (Aranda, 1994) to 40 species (Emmons, 1987). Owing to our small sample size, we may have missed some species occasionally taken by the jaguar. For example, photographic evidence from camera trapping shows that in ENP jaguars also prey on striped skunks *Conepatus semistriatus* (Figure 3.2).

The giant anteater was the dominant species both in terms of relative scat frequency and biomass consumed. The dominance of the giant anteater was not a peculiar phenomenon for a particular year, but occurred throughout all sampling periods (data not shown). Consequently, the jaguar's dietary niche was narrow – 0.104 and 0.121 for relative scat frequencies and biomass consumed, respectively. Most other jaguar diet studies reported an intermediary niche breadth close to 0.5 (Nuñez et al., 2000; Leite and Galvão, 2002; Scognamillo et al., 2003; Azevedo and Murray, 2007; Azevedo, 2008). Only Foster et al. (2009) observed a similar niche width of 0.113 in undisturbed forests in Belize, where armadillos made the largest contribution to jaguar diet.


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Figure 3.2: *Jaguar carrying a striped skunk, photographed by a camera trap in Emas National Park, central Brazil.*

Predicted and observed prey preferences

Considering foraging costs associated with searching, detecting, hunting, and handling prey, and benefits in terms of gross energy gain, we predicted the giant anteater to be the most profitable prey. With over 75 % of consumed biomass, giant anteaters were indeed the most important prey species of jaguars in ENP and based on the relatively low degree of distributional overlap between both species, they were actively selected for. Several characteristics favour the giant anteater as a high quality prey: (1) The species is highly visible in the open terrains it prefers. (2) With a body weight of 30 kg, these solitary foragers are well below a jaguar's own body weight, yet still representing a large meal. (3) Optimal foraging theory predicts that where profitable prey is very common, it will not pay a predator to lose time and energy by feeding on a less profitable prey (Emlen, 1966; McArthur and Pianka, 1966; Griffith, 1975; Krebs 1978). Indeed, as jaguar population density in ENP is very low, giant anteaters may be sufficiently abundant to become the stock prey of the jaguars. There are an estimated 20 to 40 giant anteaters per 100 km² (Miranda et al., 2006) as opposed to 0.3-0.6 jaguars per100 km² (Chapter 2). Thus, selection of giant anteaters seems to be the optimal foraging strategy for jaguars in ENP. Although generally referred to as opportunistic, some degree of feeding specialization in jaguars has been suggested before by Azevedo and Murray (2007). Indeed, all studies investigating prey selection by jaguars so far have reported some species to be taken more frequently than expected based on availability, the prey of choice generally being a medium or large mammal (Lopez-Gonzales and Miller, 2002).

The optimal foraging model further predicted the tapir to be the second most profitable prey, preferable over small mammals and peccaries. We observed similarly low contributions (6-7 % of consumed biomass) of tapir and peccary to jaguar diet. Most jaguar diet studies report the tapir as an infrequently taken prey (Novack et al., 2005), which may be a consequence of the species being much larger than the jaguar itself. Leopards similarly have been documented to show preferences towards a prey size class below 100 kg (Karanth and Sunquist, 1995; Andheria et al., 2007). Whilst this has been interpreted as a mechanism to facilitate co-existence with larger predators such as the tiger, it may also indicate a size constraint in the ability to safely capture larger prey (Karanth and Sunquist, 1995; Andheria et al., 2007). In contrast, peccaries have repeatedly been reported as an important prey species for jaguars, for example, in the Pantanal floodplains (Azevedo and Murray, 2007; Cavalcanti and Gese, 2010), the Venezuelan llanos (Polisar et al., 2003; Scognamillo et al., 2003), or the Peruvian Amazon (Emmons, 1987). Authors argued that peccaries are highly detectable, owing to their large groups and noisy foraging behaviour (Emmons, 1987; Aranda, 1994; Crawshaw, 1995). On the other hand, their large and aggressive groups pose a serious risk of injury to jaguars and they may also profit from increased vigilance (Pulliam, 1973; Lipetz and

Beckoff, 1982). For both cheetahs and lions, a preference for smaller groups of prey has been reported (Scheel, 1993; Cooper et al., 2007).

While the optimal foraging model predicted small mammals to be preferred over peccaries, they played a secondary role in jaguar diet in ENP, with a contribution to biomass of only 1.2 %. For jaguars and large predators in general, we expect small mammals to be only a supplement to a diet of medium and large mammals (Carbone et al., 1999; Lopez-Gonzales and Miller, 2002; Oliveira, 2002; Macdonald et al., 2010). Other potential large prey species not included in our rank model but common in ENP, such as the pampas deer (*Ozotocerus bezoarticus*) or the greater rhea (*Rhea americana*), are largely diurnal and group living, which may limit their availability and profitability to jaguars. Also, medium-sized species such as armadillos – main prey item in the tropical forests of Belize and Guatemala (Rabinowitz and Nottingham, 1986; Weckel et al., 2005, 2006; Foster et al., 2009) – were not detected in the jaguar diet in ENP.

Methodological considerations

Classical analyses of prey selection of large carnivores generally involve the comparison of relative frequencies of prey species in the diet with relative prey abundance (e.g., Karanth and Sunquist, 1998; Cavalcanti and Gese, 2010). Estimating prey abundance may not always be straightforward, particularly when distance sampling or capture-recapture methods cannot be applied. In the present study, we used overlap in spatial distribution between predator and prey as a proxy for prey availability. Spatial overlap with the predator is only one aspect of prey availability, and even a species with large overlap could be so rare that its availability to the predator is low. The occupancy models applied in the present study provide estimates of the probability of occurrence Ψ. The positive relationship between Ψ and abundance has often been demonstrated (e.g., Royle and Nichols, 2003). In the present case, ranking species according to their average Ψ across ENP coincides with the overlap-based ranking (data not shown). We therefore believe that distributional overlap was a reasonable proxy for prey availability. While this approach did not enable us to statistically test selectivity, it did provide evidence of selection towards giant anteaters.

Prey abundance is only one of many aspects influencing a predator's foraging behaviour. In organising available information to formulate expected prey preferences based on optimal foraging theory, we could show that selection for giant anteaters is the optimal foraging strategy for jaguars in ENP. The degree of accordance between model predictions and observed diet further demonstrated that in spite of the small data set, conclusions about prey preference based on the collected scat samples were fairly robust.

Although categorising characteristics of prey species into ranks involves subjective assessments, we chose characteristics where rank assignment could be done with minimal ambiguity. Information on body size or sociality is easily accessed in the scientific literature. Whereas we used camera trapping to evaluate distribution and abundance, other methods such as censuses of tracks or signs can be applied to obtain similar information on prey species distribution; jaguar distribution can also be inferred from the location of the scat samples themselves. Finally, information can be "borrowed" from similar study sites or species, a procedure advocated for the study of population parameters in rare or cryptic species (MacKenzie et al., 2005).

Nevertheless, the rank model has several shortcomings. The limited available information forced us to neglect several aspects involved in foraging decisions. Prey selection occurs at different levels, starting with the decision to move to a particular area for hunting (Marucco et al., 2008), or to actually hunt when prey is present (Cooper et al., 2007). In analysing scats, we were unable to assess the actual spatial and temporal circumstances of a hunt. Aspects such as the seasonal distribution of prey (Scheel, 1993; Scheel and Packer, 1995), availability of stalking cover (Schaller, 1972), or presence of competitors (Cooper et al., 2007) can influence foraging decisions by predators. We were also unable to assess individual predator characteristics such as age, sex, or reproductive status. For example, the presence of cubs (Laurenson, 1995; Cooper et al., 2007) or the sex of the predator (Caro, 1994; Cooper et al., 2007) influenced foraging behaviour of cheetahs and lions. Genetic analyses of scats could in principle determine the sex of the jaguar and its individual identity. In the present case this was only possible for seven samples which could be attributed to three individual males (JCF, unpublished data). Furthermore, prey selection of a predator may focus on particular sex or age classes within a species, or on particular prey size classes irrespective of species (Fitzgibbon and Fanshaw, 1989; Karanth and Sunquist, 1995). However, many of these aspects can only be investigated by direct observation of hunts (Cooper et al., 2007) or the sampling of kills (Cavalcanti and Gese, 2010). Direct observations are limited to very few chance encounters for the nocturnal and secretive jaguars, and to sample an adequate number of confirmed jaguar kills, animals need to be followed by continuous telemetry. Subdivision of prey species categories into age and sex classes or the analysis of sex-specific and individual-specific foraging tactics pose analytical problems for scat-based investigations and require considerably larger samples than available in the present study.

A key assumption in the optimal foraging model is that all considered aspects contribute equally to foraging costs. It could be argued that search costs or the risk of a failed hunt may have a stronger influence on jaguar foraging behaviour than prey detectability. Nevertheless, there is no doubt that the profitability of a prey species is influenced by a whole range of species-specific (size, sociality) and study site-specific (distribution, abundance) characteristics. This implies that considering only abundance as a measure of availability, as is often done, is not sufficient to explain predator foraging ecology. It may even lead to misdirected conservation efforts if management of the prey base is a predator conservation strategy.

Implications for jaguar conservation and conclusion

Using readily available information about prey species, we assessed their availability for and vulnerability to jaguar predation in ENP and predict prey preferences. Our model is limited in terms of quantitative predictions but ranking the available information creates a robust qualitative model. Our prediction of the giant anteater being the most profitable prey explains the selective tendencies of the jaguar towards this species. The giant anteater is also common and widespread in the surrounding areas of the park (Vynne et al., 2010). Thus, jaguar persistence in the region of ENP is unlikely to be threatened by scarceness of adequate prey.

The jaguar’s flexibility to adapt its foraging behaviour to a site specific prey base is an advantage for survival in altered landscapes (Foster et al., 2009) but it also predisposes the species to conflicts with humans. In areas where medium and large sized prey species are scarce, jaguars can substitute their diets with domestic livestock (Foster et al., 2009). In areas rich in natural prey, such as the Pantanal floodplains, jaguars also incorporated cattle in their diet (e.g., Azevedo and Murray, 2007; Cavalcanti and Gese, 2010). The resulting conflict can directly impact jaguar populations through retaliatory hunting or indirectly affect their conservation by creating negative attitudes towards the species (Woodroffe and Ginsberg, 1998). In this study, we only recorded a single incidence of jaguar predation on cattle. Given that the study region is dominated by crop plantations, and livestock ranching is restricted, this was not surprising. Cattle ranchers of the region reported more problems with livestock predation by puma (Furtado, unpublished data) and overall perception of the jaguar by the local community was positive (Santos et al., 2008). Thus, conflict with cattle ranchers because of predation on livestock does not seem to be a major problem. Considering that the jaguar population of ENP already faces a risk of extinction simply owing to its small size and high degree of isolation (Silveira and Jácomo, 2002), these findings are likely to help regional jaguar conservation.

Acknowledgements

This study received financial support from the Disney Worldwide Conservation Fund, Fundação Monsanto, the Earthwatch Institute, the Memphis Zoo, the Leibniz Institute for Zoo and Wildlife Research, and Idea Wild. RS received a scholarship from the German Academic Exchange Service (DAAD). We thank ICMBio for granting permission to work in ENP and ENP management for logistical support. We thank the kennels Canil Caraíbas and HR for their technical support regarding the scat detector dogs. We are indebted to the entire Jaguar Conservation Fund team, all Earthwatch volunteers and interns, and especially Raphael Almeida, Tiago Boscarato and Grasiela Porfírio for help with field work and scat analysis. We thank Mirjam Nadjafzadeh for comments on the manuscript.

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Supplementary material

I: Joint occupancy model of jaguars and their prey

To model occupancy patterns of the jaguar and its main prey species in ENP, we divided our 3-month camera trapping period into five 16-day 'occasions' and noted for each trap site and each occasion whether each species had been photographed or not. We modelled both jaguar and prey occupancy $\boldsymbol{O}$ as a function of the distance to the nearest water course (***DIST***), percentage of dense habitat (forest and scrublands as opposed to the open grasslands and swamps) in a 1,750-m buffer around the camera trap (***DENSE***), and a random spatial effect $\boldsymbol{e}$ to account for spatial autocorrelation in occupancy. We further modelled detection probability as a function of camera trap placement on or off-road ($\boldsymbol{r}$, a binary vector of 1 for on road locations and 0 otherwise). We coupled each of the prey species models with the jaguar model to estimate the number of sites where both species co-occurred. Let $\boldsymbol{j}$ be a species vector containing the jaguar and a single given prey species. The full joint occupancy model then reads:

$$O_{ji} = \text{Bernoulli}(\Psi_{ji});$$
$$\text{Logit}\ (\Psi_{ji}) = \alpha_j + \beta 1_j * DIST_i + \beta 2_j * DENSE_i + e_{ji};$$
$$y_{ji} = \text{Binomial}(p_j[r_i], x_i);$$
$$J = \sum \boldsymbol{O_1};$$
$$P = \sum \boldsymbol{O_2};$$
$$B = \sum(\boldsymbol{O_1} * \boldsymbol{O_2});$$
$$Olap = B/J * 100$$

where Ψ_{ji} is the probability of occupancy of species j at site i, α_j is the intercept of the logit linear regression on Ψ_{ji}, $\beta 1_j$ and $\beta 2_j$ are the species-specific regression coefficients for the respective covariates, y_{ji} is the number of visits during which species j was detected at site i and x_i is the total number of visits made to site i. J, P, B and $Olap$ are derived quantities and represent the number of sites occupied by jaguars (J), the number of sites occupied by the prey species (P), the number of sites occupied by both species (B) and the percentage of jaguar-occupied sites that is also occupied by the respective prey species, or distributional overlap ($Olap$).

We implemented the model in the software WinBUGS (the WinBUGS pseudo code for the model is shown in Figure 3.S1), accessed through the program R, version 2.10.1 (R Development Core Team, 2009) using the package R2WinBUGS (Sturtz et al., 2005). WinBUGS uses Gibbs sampling, a Markov chain Monte Carlo (MCMC) method simulating samples from the joint posterior distribution of the unknown quantities in a statistical model (Casella and George, 1992). MCMC chains are started at arbitrary parameter values and since successive iterations depend on the outcome of the previous iteration, the start value will be reflected in a number of initial iterations that should be discarded (the burn-in). This characteristic can also lead to autocorrelation of successive iterations. To avoid autocorrelation, a thinning rate is specified as every i^{th} iteration used in the characterization of the posterior distribution of the parameters. We ran three MCMC chains with 5,000 iterations, a burn-in of 1,000 and a thinning rate of three. This combination of values ensured an adequate number of iterations to characterize the posterior distributions, that MCMC chains showed no indications of autocorrelation or effects of the initial values, and that all chains converged (i.e. oscillated around essentially the same mean parameter value). We checked for chain convergence using the Gelman-Rubin statistic (Gelman et al., 2004), R-hat, which compares between and within chain variation. R-hat values below 1.1 indicate convergence (Gelman and Hill, 2006). Values for all estimated parameters were below 1.1.

Single-season occupancy models assume that the occupancy state of a sampling unit does not change over the course of the study (MacKenzie et al., 2006). At the scale of the present study, where occupancy may largely depend on the movement of a single individual, it is arguable that the species might temporarily not be available for sampling at a given camera trap. However, we interpreted the pooled data from 16 consecutive sampling days as single visit to the sampling unit. We believe that at some point within this time frame an individual should be available for sampling if the sample unit lies within its home range.

As our main objective is a description of the distribution of species and not an extrapolation to other areas, we did not engage in determining the best or most parsimonious model for each species, but only considered the most general model for all species. Exploratory data analysis showed that model results were robust to the removal or addition of covariates.

```
model{

#jaguar occupancy model
for (i in 1:nsites) {
r[i]<-roads[i]+1
zJ[i]~dbern(psiJ[i])
lpsiJ[i]<-aJ+bJ*Dist[i]+cJ*Dense[i]+eJ[i]
psiJ[i]<-exp(lpsiJ[i])/(1+exp(lpsiJ[i]))
J[i]<-zJ[i]+1
ObsJ[i]~dbin(pJ.eff[i], Tx)
pJ.eff[i]<-pJ[r[i]]*zJ[i]

#prey occupancy model
zP[i]~dbern(psiP[i])
lpsiP[i]<-aP+bP*Dist[i]+cP*Dense[i]+eP[i]
psiP[i]<-exp(lpsiP[i])/(1+exp(lpsiP[i]))
P[i]<-zP[i]+1
ObsP[i]~dbin(pP.eff[i], Tx)
pP.eff[i]<-pP[r[i]]*zJ[i]

both[i]<-zJ[i]*zP[i]      # site occupancy status by both species
}

#Priors for coefficients of jaguar occupancy model
aJ~dflat()
bJ~dnorm(0, 0.1)
cJ~dnorm(0, 0.1)
pJ[1]~dunif(0,1)
pJ[2]~dunif(0,1)

#priors for prey occupancy model
aP~dflat()
bP~dnorm(0, 0.1)
cP~dnorm(0, 0.1)
pP[1] ~dunif(0,1)
pP[2] ~dunif(0,1)

#Gaussian CAR priors for spatial random effects
e[1:nsites] ~ car.l1(adj[], weights[], num[], 0.75)
eP[1:nsites] ~ car.l1(adj[], weights[], num[], 0.75)
for(k in 1:sumNumNeigh) {
weights[k] <- 1
}

#derived quantities – number sites occupied by jaguars (1), prey (2) and both (3)
zJtot<-sum(zJ[1:119])
zPtot<-sum(zP[1:119])
btot<-sum(both[1:119])

}
```

Figure 3.S1: Pseudo-code to implement joint jaguar-prey occupancy model in WinBUGS.

II. Ranking of prey species for the optimal foraging model

a) Difference in distribution between jaguars and prey species

To express how much the distribution of a prey species overlapped with the distribution of the jaguar, we estimated the percentage of sites occupied by jaguars that were also occupied by a given prey species with the occupancy model. We assumed that search costs increase with decreasing distributional overlap (Table 3.S1).

Table 3.S1: *Ranking of search costs of jaguar prey species in Emas National Park, central Brazil. F: average number of photographs at sites where species co-occurs with the jaguar; HR: average home range size; C/HR: average number of cameras present in an average circular home range;* F_c*: F corrected for the number of cameras per home range; p(D): ranking of relative probability of detection.* R_A*: resulting abundance rank (1 = abundant, 4 = rare).* R_D*: rank describing overlap in distribution (1=high, 4=low); sum: sum of* R_A *and* R_D*;* R_S *= overall search cost rank.*

Species	**F (SD)**	**HR [km²]**	**C/HR**	**F_c (SD)**	***p(D)***	**R_A**	**R_D**	**Sum**	**R_S**
Tapir	3.18 (0.17)	16.8 [1]	1.2	2.65 (0.14)	3	2.5	1	3.5	1
Peccary	1.17 (0.19)	55.5 [2]	3.9	0.30 (0.05)	4	4	2	6	4
Giant anteater	2.28 (0.23)	8.96 [3]	1	2.28 (0.23)	2	2.5	3	5.5	3
Agouti /Opossum	1.19 (0.37)	0.02-0.085[4,5]/ 0.001 [6]	1	1.261 (0.33)	1	1	4	5	2

[1] JCF, unpublished data; [2] Jácomo, 2004; [3] WCS, no date; [4] Aliaga-Rossel et al., 2008 [5] Silvius and Fragoso, 2003; [6] Almeida et al., 2008.

b) Abundance of prey species

We evaluated species abundance based on the average number of photographs at sites where it was found or estimated by the occupancy model to co-occur with the jaguar. Since in this context abundance is thought to influence the encounter probability between the jaguar and a prey, peccary abundance is interpreted as abundance of peccary groups, not individuals. Based on their average home range size (Table 3.S1), camera traps represent for agoutis, opossums and giant anteaters, – mostly – independent sample sites. Each individual tapir or peccary group, however, likely contributes to photo-counts at several neighbouring traps, inflating the total number of photographs. To correct for this autocorrelation, we calculated the average number of traps contained in an average tapir and peccary home range and divided their total number of photographs by this number. We obtained the average number of traps per home range by randomly placing 1,000 circular home ranges on our trapping grid, counting the number of cameras within, and averaging over the 1,000 ranges. Corrected average numbers of photographs were assessed against a subjective evaluation of the probability of detection of the species by camera traps: Tapirs move much on roads and trails where cameras are usually set up (Harmsen et al., 2009), whereas peccaries and giant anteaters, preferring more open habitats, have a bigger chance of moving through the vegetation instead of on the road. On the other hand, peccaries move in large groups (Reis et al., 2006), increasing group detection probability. We therefore think that peccary groups have the highest detection probabilities, followed by tapirs, then giant anteaters. Detection probability of small mammals, which move through the vegetation more freely and may be missed simply due to small body size, is lower still. We established the final search cost rank based on the sum of the partial ranks (Table 3.S1).

c) Detectability of a prey species

We established a detectability rank based on species-specific degree of sociality (solitary – higher costs, social – lower costs), body size (<5 kg – highest costs, 5-15 kg – medium costs, >15 kg – lowest costs), and habitat preferences as estimated in the occupancy model (closed habitat – highest costs, no clear preference – medium costs, open habitat – lowest costs). We established the final detection rank based on the sum of the three partial ranks (Table 3.S2).

Table 3.S2: *Ranks describing the degree of sociality, body size (Size), habitat preference as established by the occupancy model (see Table 3.2), and resulting detectability rank for jaguar prey species in Emas National Park, central Brazil.*

Species	Sociality[1]	Size [1,2]	Habitat preference	Sum	Rank
Tapir	3	2	4	8.5	3
Peccary	1	2	2.5	5.5	1
Giant anteater	3	2	1	6	2
Agouti/Opossum	3	4	2.5	9.5	4

[1] Reis et al., 2006; [2] JCF, unpublished data

d) Probability of failed hunts

We evaluated the probability of a hunting attempt to fail based on prey sociality and body size relative to the jaguar. We categorised prey species as living in groups (high probability of failed hunts), or solitary (low probability). We categorised prey body size as larger than the jaguar (high probability), smaller than the jaguar but large >15 kg (medium probability), medium or small <15 kg (low probability). We established the final detection rank based on the sum of the partial ranks (Table 3.S3, literature consulted is the same as in Table 3.S2).

Table 3.S3: *Ranks describing the degree of sociality and body size relative to jaguar body size (Rel. size) of main prey species, and resulting rank for the probability of failed hunts by jaguars in Emas National Park, central Brazil.*

Species	Sociality	Rel. size	Sum	Rank
Tapir	2	4	6	3
Peccary	4	2.5	6.5	4
Giant anteater	2	2.5	4.5	2
Agouti/Opossum	2	1	3	1

e) Risk of injury

We ranked risk of injury based on prey size and sociality (as under d), and the presence of tusks or claws adding to the ability of a prey species to inflict injuries (present – high risk, absent – low risk). We established the final risk rank based on the sum of the partial ranks (Table 3.S4, literature consulted is the same as in Table 3.S2).

Table 3.S4: *Ranks describing the degree of sociality, body size relative to jaguar body size (Rel. size), presence of tusks or claws, and resulting rank for the risk of injury to a jaguar when hunting its main prey species in Emas National Park, central Brazil.*

Species	Sociality	Rel. size	Tusks/claws	Sum	Rank
Tapir	2	4	3	9	3
Peccary	4	2.5	3	9.5	4
Giant anteater	2	2.5	3	7.5	2
Agouti/Opossum	2	1	1	4	1

f) Handling time

We established handling time ranks assuming that it increases with prey body size as under d (Table 3.S5, literature consulted is the same as in Table 3.S2).

Table 3.S5: *Handling time ranks and gross energy gain ranks for main prey species of the jaguar in Emas National Park, central Brazil, based on body size relative to jaguar body size.*

Species	Handling time	Gross energy gain
Tapir	4	3.5
Peccary	2.5	2
Giant anteater	2.5	3.5
Agouti/Opossum	1	1

g) Gross energy gain

Over the range of some body masses, the gross energy gain increases with prey body mass. However, the amount of meat a predator can actually ingest from a single kill will level off at some prey mass owing to spoilage, i.e. losses to scavengers or decay (Ackerman et al., 1986; Foster et al., 2009). While there is no information about the prey body mass at which the energetic gain to a jaguar reaches an asymptote, a study by Cavalcanti and Gese (2010) investigating the time between consecutive kills of jaguars showed that time intervals first increased with increasing body size and then levelled off at 30 kg. Whilst this time interval does not necessarily equal the time a cat feeds on the carcass, occasional observations of jaguars at kills confirm that the individuals indeed return to a kill to feed repeatedly over several days (JCF, unpublished data). We used this information to construct the following gross reward ranking: <5kg – lowest gain; based on an energetic model for cougars by Ackerman et al. (1986), the average daily energetic requirements of a felid the size of a jaguar are likely not met by feeding on such a small prey; 5-15 kg – medium-low gain, 15-30 kg – medium-high gain; >30 kg – highest gain (Table 3.S5).

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CHAPTER 4

Using hierarchical Bayesian modelling of site occupancy under imperfect detection to investigate resource partitioning between two sympatric large predators, the jaguar and puma in central Brazil

Abstract

Coexistence of sympatric species is mediated by resource partitioning of food, time and space. Pumas *Puma concolor* occur sympatrically with jaguars *Panthera onca* throughout most of the jaguar’s range. Owing to its size, the jaguar is thought to be the dominant species and avoided by the puma but few studies have explicitly investigated the effect of jaguar presence on puma occurrence. Here, we use camera trapping and occupancy models that account for imperfect detection in a Bayesian framework to investigate differences in habitat use and space partitioning between jaguars and pumas in Emas National Park (ENP), central Brazil. Jaguars were estimated to occupy 54.1 % and pumas 44.8 % of the park. Jaguar occupancy was negatively correlated with distance to water and positively correlated with the amount of dense habitat in the vicinity of the camera trap. Both species were less often present at the same site than expected under independent distributions. Puma occupancy was negatively correlated with jaguar presence, and pumas had a higher detection probability at off road camera traps than jaguars, suggesting that pumas avoided major travel routes of and sites occupied by jaguars. In contrast, pumas occur frequently beyond the park border where jaguars are less frequently present although they were the dominant competitor where habitat conditions are favourable. We conclude that the small and confined jaguar population of ENP is more likely to be susceptible to stochastic events than the puma population which extends beyond the park.

Key words: Cerrado, distribution, habitat use, *Panthera onca*, *Puma concolor*, space partitioning

Introduction

Differences between sympatric species in the use of trophic, temporal and spatial resources are thought to promote species co-existence in ecological systems (Schoener, 1974). For sympatric carnivores with similar morphology and foraging strategies, variation in body mass, often correlated with prey body mass (Carbone and Gittleman, 2002), can reduce competition for trophic resources (Rosenzweig, 1966; Karanth and Sunquist, 1995). Partitioning of food resources also takes place between similar sized carnivores (e.g., Kruuk et al., 1994; Jácomo et al., 2004). For species with similar feeding habits, the partitioning of habitat (Jácomo et al., 2004) or, more generally, space (Creel and Creel, 1996; Palomares et al., 1996; Durant, 1998), as well as differences in activity patterns (Karanth and Sunquist, 2000; Romero-Muñoz et al., 2010) can facilitate co-existence.

The jaguar *Panthera onca* (Linnaeus, 1758) is the largest neotropical felid. Having experienced a range contraction of almost 50 % over the last century (Zeller, 2007) the species is classified as Near Threatened with decreasing population trends (IUCN, 2010). Throughout most of its distribution, the species occurs sympatrically with the puma *Puma concolor* (Iriarte et al., 1990). Although listed as Least Concern, puma population trends are also decreasing (IUCN, 2010). Very little is known about the species in the neotropical part of its distribution (Kelly et al., 2008).

Owing to its larger size, the jaguar is thought to be competitively dominant over the puma (Schaller and Crawshaw, 1980; Crawshaw and Quigley, 1984). The puma is thought to be more flexible and a super-generalist in its food and space use habits (Iriarte et al., 1990). Several authors report avoidance of jaguars by pumas on a local scale in both spatial and temporal terms (Emmons, 1987; Scognamillo et al., 2003; Harmsen et al., 2009; Romero-Muñoz et al., 2010). Consequently, pumas seem to be rare where jaguars are abundant (Rabinowitz and Nottingham, 1986; Azevedo and Murray, 2008) and vice versa (Noss, 2006; Kelly et al., 2008).

Partitioning in space can be achieved either through evolved differences in species-specific habitat preferences (Núñez et al., 2000), or by active avoidance of the actual presence of competitor individuals, for example by using olfactory cues. Recently, two camera trapping studies assessed puma habitat and space use with respect to detection of jaguars (Harmsen et al., 2009; Foster et al., 2010) and found that both species were largely detected at the same trapping sites and that their photographic counts correlated.

These studies used raw photographic data to reach their conclusions; none explicitly considered jaguar presence in a formalized modelling framework for puma space use. The use of raw photographic data to investigate abundance, intensity of space use or occurrence of species can lead to biased results if analyses do not account for imperfect detection that possibly is species-specific and varies in space (MacKenzie et al., 2006; Royle and Dorazio, 2008). Hierarchical models explicitly describe the observation process, detection by camera trap or any other means, separately from the underlying ecological process – the actual distribution of occurrence, abundance and so on (Royle and Dorazio, 2008). Here we use camera trapping data and Royle and Dorazio's (2008) hierarchical formulation of the occupancy models developed by MacKenzie et al. (2006) as implemented in a Bayesian framework to investigate differences in habitat use and patterns of co-occurrence of the jaguar and the puma in Emas National Park (ENP), central Brazil. The park is one of the last refuges for both species in the central Brazilian Cerrado grasslands, one of the world's 25 ecological hot spots (Myers et al., 2000). In spite of a severe threat of large scale habitat loss, both species remain very little studied in this biome. The applied models provide a straight-forward approach to the question of space partitioning between sympatric species.

Material and methods

Study area

Emas National Park, listed as a Human Heritage Reserve by UNESCO, is located in south-western Goiás state (18º 19'S, 52º 45'W; Figure 4.1) in the Cerrado savanna of central Brazil. The park has a size of 1,320 km² and protects large tracts of grassland plains (97 %), small patches of shrub fields (1 %), marshes, and riparian forest (2 %). During the wet season (October to March), rainfall averages 1,500 mm. There is very little precipitation during the rest of the year, when daytime temperatures can reach 40° C and night temperatures may drop to -1.5° C (IBDF/FBCN, 1981). ENP is situated in a highly productive agricultural area. Large-scale soybean, corn and sugar cane plantations dominate and fragment the regional landscape. This situation is typical of the Cerrado: Brazil's second largest biome covers 21 % of the country's area but over the last 35 years more than half of it was transformed into cultivated land (Klink and Machado, 2005). Today, only 1.9 % is strictly protected and 80 % is considered degraded (Cavalcanti and Joly, 2002).

Camera trapping

Between March and June 2008, we deployed 119 camera trap stations on a park-wide 3.5 x 3.5 km grid to estimate jaguar abundance and density in the study area (Chapter 2). Cameras were set along park roads and, at off-road locations, along game trails. Each station consisted of two camera traps of the 35-mm LeafRiver C1-BU type (Vibrashine Inc., Taylorsville, MS

3968, USA) facing each other with a lateral offset of approximately 30 cm to avoid flash interference. Camera traps were strapped to trees or stakes approximately 40-50 cm above ground. During the three months of sampling camera traps were checked at 10-14-day intervals for film roll and battery replacement. Since cameras were easily triggered by sunlight in the predominately open habitat of ENP, we programmed cameras to work 24h/day in shady locations and only during night time in exposed locations. As in ENP both investigated species are predominantly nocturnal (Silveira, 2004) the effect on data should be minimal.

Occurrence model

To model occupancy patterns of the jaguar and puma in ENP, we divided our 3-month camera trapping period into five 16-day 'occasions' and noted for each trap site and each occasion whether the species had been photographed or not. We analyzed data using occupancy models (MacKenzie et al., 2006). These models can be formulated as hierarchical models (Royle and Dorazio, 2008) where the true occupancy state O_i (1 if present and 0 otherwise) of a sampling unit i is the outcome of a Bernoulli trial with probability of occupancy Ψ:

$$O_i \sim \text{Bernoulli}(\Psi).$$

Since non-detection of a species at a sampling unit can either be caused by true absence or by failure of detection, repeated visits to sampling units, x_i, are used to estimate detection probability p conditional on occupancy. The number of visits during which the species was detected at site i, y_i, is a random binomial variable with probability of detection p and number of trials x_i.

$$y_i \sim \text{Binomial}(p, x_i).$$

Using a logit link function on Ψ or p, both parameters can be modelled as linear functions of independent variables, as in regular logistic regression models (MacKenzie et al., 2006).

The occupancy state $\boldsymbol{O}$ – also termed occurrence or presence, we use these terms synonymously in the remainder of the paper – is a partially latent variable: based on our observations we can only classify sites where the species was observed at least once as occupied without error. Implementation of the model in a Bayesian framework explicitly estimates the latent $\boldsymbol{O}$ (MacKenzie et al., 2006; Royle and Dorazio, 2008), is straightforward and allows the definition of functions of the estimated occupancy state (MacKenzie et al., 2006). Thus, this approach enabled us to estimate the number of sites occupied by jaguars (J), pumas (P) and both species (B) as

$$J = \sum \boldsymbol{O_J};\ P = \sum \boldsymbol{O_P};\ B = \sum(\boldsymbol{O_J} * \boldsymbol{O_P}),$$

where the subscripts "J" and "P" denote parameters for jaguars and pumas, respectively. We were interested in determining whether both species co-occurred more or less often than expected under the assumption that their distributions are independent. Two species, A and B, occur independently if the probability of occurrence of both species Ψ(A and B) = Ψ(A)*Ψ(B). Thus, the expression φ = Ψ(A and B) / Ψ(A)*Ψ(B) describes the degree of spatial interaction of both species. If $\varphi > 1$, species co-occur more often than expected; if $\varphi < 1$, species co-occur less often than expected (MacKenzie et al., 2006). In our approach, we used the actual rates of occurrence of jaguars and pumas, J_r and P_r, as the percentage of all sites occupied instead of the probability of occurrence Ψ. We defined $J_r = J/N$, $P_r = P/N$ and $B_r = B/N$, where N is the total number of sampling sites, and

$$\varphi = B_r/J_r * P_r.$$

We separately modelled both jaguar and puma occupancy $\boldsymbol{O}$ as a function of the distance to the nearest water course ***Dist*** and percentage of dense habitat ***Dense*** (forest and scrublands as opposed to the open grasslands and swamps) in a 1,750-m buffer around the camera trap. This corresponded to half the average distance between neighbouring traps. For pumas, we added the jaguar occupancy state $\boldsymbol{O_J}$ as a binary covariate. Owing to our sampling design and the mobility of the studied species, occupancy states could be spatially autocorrelated. To account for possible spatial autocorrelation, we defined the neighbourhood of each sampling site as all camera traps within a 7-km radius and added a random spatial effect to the linear predictor of logit($\boldsymbol{\Psi}$), with its value at site i, e_i, being conditional on the value of $\boldsymbol{e}$ at all neighbouring sites, corresponding to a conditional autoregressive (CAR) model (Besag et al., 1991). Since Moran's I (Cliff and Ord, 1973) of model residuals calculated following Moore and Swihart (2005) was not significant for neighbourhood distances between 5 and 52 km, we concluded that this approach was sufficient to correct for the actual spatial autocorrelation in the data. For both species we modelled detection probabilities $\boldsymbol{p_J}$ and $\boldsymbol{p_P}$ as functions of camera trap placement on or off road ($\boldsymbol{r}$, a binary vector of 1 for on-road locations and 0 otherwise). For pumas, we further included $\boldsymbol{O_J}$ as a possible covariate on $\boldsymbol{p_P}$.

We implemented the full model in the software WinBUGS accessed through the program R, version 2.10.1 (R Development Core Team, 2009) using the package R2WinBUGS (Sturtz et al., 2005). WinBUGS uses Gibbs sampling, a Markov chain Monte Carlo (MCMC) method simulating samples from the joint posterior distribution of the unknown quantities in a statistical model (Casella and George, 1992). We report the mean, standard error (SE) and, for some parameters, the 2.5 and 97.5 percentiles (Bayesian equivalent to 95 % confidence interval – BCI) of the posterior distributions of the estimates. The model code and run specifications are detailed in the supplementary material. We mapped jaguar and puma rates of occurrence as the average of $\boldsymbol{O_J}$ and $\boldsymbol{O_P}$ over all MCMC iterations in 3.5 x 3.5 km grid cells covering ENP. To this end, we calculated for each grid cell the percentage of dense habitat and distance to water from the centre of the cell, and included predictions of $\boldsymbol{O_J}$ and $\boldsymbol{O_P}$ based on the logistic regression parameters described above in our WinBUGS model code.

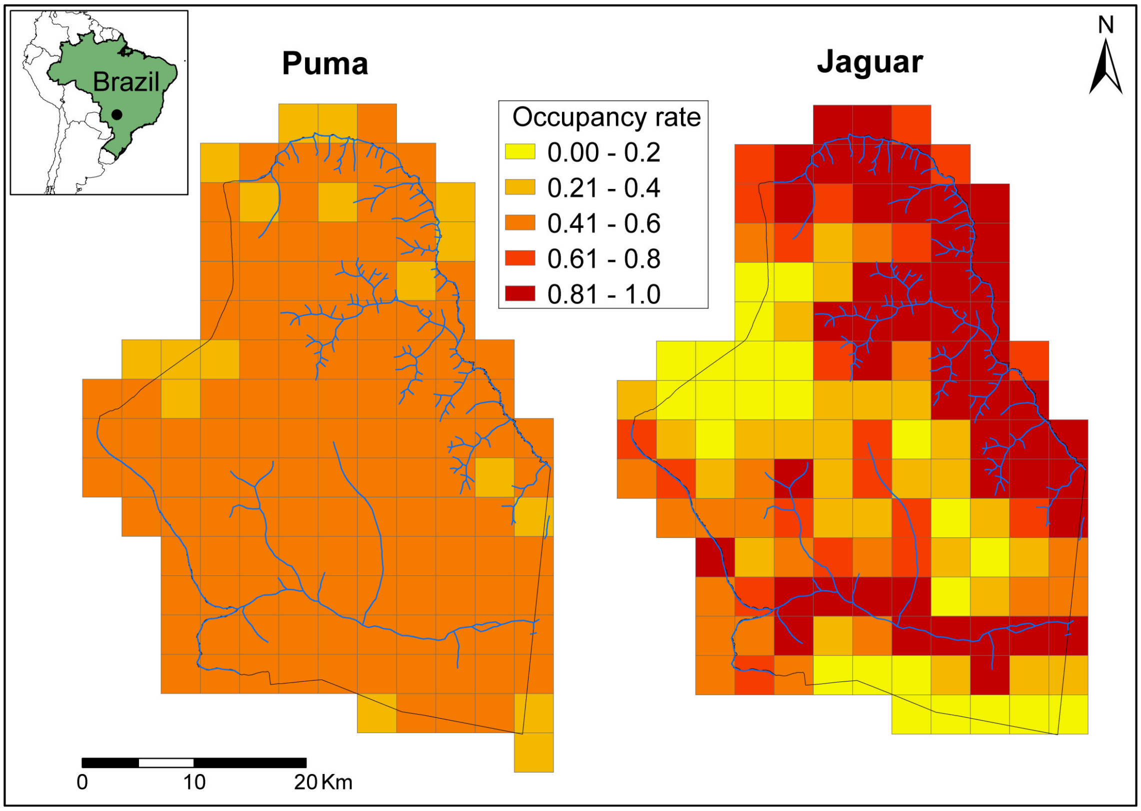

Fig. 4.1: *Rate of occupancy of the jaguar and puma in Emas National Park, central Brazil; the species' occupancy states (0 or 1) are estimated per each 3.5 x 3.5 km grid cell as a species specific function of percentage of dense habitat and distance to water from the cell's centre, and for the puma, of jaguar occupancy. Rate of occupancy is the average occupancy state over 5,000 MCMC iterations of the model run in WinBUGS. Water courses of the park are shown in blue.*

Results

We detected jaguars at 37 (31.1 %), pumas at 35 (29.4 %) and both species together at 9 (7.6 %) of 119 sample sites. The number of sites estimated to be occupied was 64.3 ± 4.7 (54.1 %) for jaguars, 53.3 ± 8.6 (44.8 %) for pumas and 22.5 ± 6.8 (18.87 %) for both species together.

The degree of spatial interaction between jaguars and pumas, φ, was 0.77 ± 0.13 (95 % BCI: 0.54-1.06).

***Table 4.1**: Parameter estimates (with standard errors – SE) from the joint occupancy model for jaguars and pumas in Emas National Park, central Brazil; β = coefficients of logistic regression on probability of occurrence Ψ; Dist = Distance to nearest water course; Dense = percentage of dense habitat in a 1,750-m buffer; O_J = estimated occurrence of jaguar (0 or 1); p = detection probability.*

Species	**Parameter**	**Estimate (SE)**	**2.5 %**	**Median**	**97.5%**
Jaguar	$\beta(Dist)$	-1.47 (0.52)	-2.6	-1.42	-0.57
	$\beta(Dense)$	1.20 (0.77)	-0.12	1.14	2.89
	p (*off road*)	0.05 (0.02)	0.02	0.05	0.10
	p (*on road*)	0.37 (0.04)	0.29	0.37	0.46
Puma	$\beta(Dist)$	-0.44 (0.43)	-1.28	-0.46	0.44
	$\beta(Dense)$	0.03 (0.39)	-0.72	0.04	0.84
	$\beta(O_J)$	-1.47 (0.87)	-3.11	-1.48	0.31
	p (*off road*)	0.17 (0.06)	0.08	0.17	0.32
	p (*on road*, O_J=0)	0.23 (0.05)	0.14	0.28	0.34
	p (*on road*, O_J=1)	0.25 (0.08)	0.11	0.25	0.42

Jaguar occurrence was negatively correlated with distance to water and positively correlated with the percentage of dense habitat (Table 4.1). Puma occurrence showed a negative correlation with jaguar occurrence, a weak negative correlation with distance to water and no correlation with percentage of dense habitat (Table 4.1). Consequently, predicted jaguar occupancy rates showed a distinct pattern to be higher along the watercourses of the park, while puma occupancy rates were more uniform and overall lower across the park (Figure 4.1).

Jaguar detection probability was 0.05 ± 0.02 and 0.37 ± 0.04 off and on roads, respectively. Puma detection was lower off road (0.17 ± 0.06), but similar on roads with (0.25 ± 0.08) and without jaguar presence (0.23 ± 0.05).

Discussion

Space partitioning is one mechanism promoting the co-existence of sympatric carnivores with similar feeding habits (Palomares et al., 1996; Durant, 1998; Jácomo et al., 2004). Although the distributions of the jaguar and puma in the study area overlapped considerably (40 % of the puma's distribution was occupied by jaguars, and 35 % of the jaguar's distribution was occupied by pumas), the investigated habitat characteristics affected their occurrence in different ways. Jaguar occurrence increased with decreasing distance to water and increasing amount of dense habitat. The close association of the species with water has been documented before (Mondolfi and Hoogesteijn, 1986) and even from habitats dominated by water, such as the Amazon rainforest (Emmons, 1987) or the Pantanal floodplains (Crawshaw and Quigley, 1991). In contras, the puma was more of a habitat generalist. For both regression coefficients, BCI widely overlapped with 0, providing little support for correlation of puma occurrence with distance to water or amount of dense habitat (Table 4.1). Pumas are found in a wider range of habitats than jaguars, both across their distribution (Sunquist and Sunquist, 2002) and in regions where both species co-occur (Leite and Galvão, 2002). The species tends to prefer more open and drier habitats (Polisar et al., 2003; Núñez et al., 2000). However, overall habitat use by both cats is similar where sympatric (Schaller and Crawshaw, 1980; Taber et al., 1997; Scognamillo et al., 2003; Hernandéz, 2008; Harmsen et al., 2009; Foster et al., 2010).

None of the above studies explicitly included the presence of jaguars as an explanatory variable for puma occurrence. We observed a strong negative correlation of puma occurrence with jaguar presence (Table 4.1). Since we also accounted for differences in habitat use by the species in our regression, this indicated active spatial avoidance of jaguars by pumas. This is corroborated by the measure of spatial interaction of both species, φ: With a value of 0.77 φ was well below 1, the value expected under independent distributions. Whilst the 95 % BCI included 1, most of the density of the posterior distribution of φ was located away from 1 (Table 4.1).

Puma detection probability on roads was not influenced by presence of jaguars. However, puma detection probability off road was much higher than jaguar detection probability off road. This also indicates a shift of puma movement activity away from the major travel routes of jaguars in areas shared by both species.

Most studies of co-existence between jaguars and pumas investigated differences in diet. Both species can prey on large animals; food niches therefore sometimes show considerable overlap (Aranda and Sánchez-Cordero, 1996; Taber et al., 1997). Owing to their smaller size, pumas are generally thought to be able to base their diet to a larger extent on smaller species (Emmons, 1986; Nuñez et al., 2000; Leite and Galvão, 2002; Scognamillo et al., 2003). Our results suggest that the variation in diet overlap between jaguars and pumas reported by previous studies may be influenced by the differences in habitat preferences (or lack of them) between prey species of common interest to both predators. Such variation in diet overlap may be pronounced if prey species show distinct habitat preferences and their favourite habitats were factually inaccessible to pumas because they were preferentially occupied by jaguars. Alternatively, if there is little variation in habitat preferences amongst key prey species, temporary or permanent lack of access to specific localities or habitats by pumas will not be reflected in the diet of either predator. It seems therefore prudent to argue that diet overlap should always be complemented by information on spatial or temporal segregation of sympatric carnivores, particularly if they have roughly similar body sizes and are flexible in their choice of prey. Otherwise diet overlap is unlikely to provide either sufficient evidence on niche partitioning nor likely to detect the mechanism by which this may be achieved.

Few authors found strong evidence for temporal segregation through distinct daily activity patterns (Monroy-Vilchis et al., 2009; Romero-Muñoz et al., 2010) and in most studies, activity patterns of both species were similar (Polisar et al., 2003; Scognamillo et al., 2003; Harmsen et al., 2009), including in ENP (Silveira, 2004). Harmsen et al. (2009) suggested that pumas avoided jaguars spatio-temporally, as intervals between subsequent camera trap pictures of jaguars and pumas at a trap site were significantly larger than between subsequent jaguar-jaguar and puma-puma pictures. Whilst it would be interesting to look at spatio-temporal patterns of species detection on a daily basis, our data were too sparse to estimate parameters of detection and presence at this resolution. Also, single-season occupancy models such as the ones applied here assume that the true occupancy state of a sample unit does not change over the course of the study (MacKenzie et al., 2006). At the scale of the present study, where the occupancy state of a given sampling unit may largely depend on the within-home range movements of a single individual, the species might temporarily not be available for sampling at a given camera trap. Therefore, we interpreted the pooled data from 16 consecutive sampling days as a single visit to the sampling unit and assumed that at some point within this time frame an individual should be available for sampling if the sample unit lies within its home range. This assumption would not be reasonable for the interpretation of one day as one visit.

Methodological considerations

By applying the Bayesian formulation of a two-species occupancy model, we investigated habitat associations of and spatial interactions between jaguars and pumas in ENP whilst simultaneously accounting for imperfect species detection, differences in detection probabilities between species, and differences in detection owing to camera trap placement. It is intuitive that ignoring imperfect detection leads to an underestimate of the area occupied by the species of interest. But detection also varied spatially and between species. Whilst pumas had a slightly lower detection probability than jaguars, both species were more readily detected at on-road locations. This is expected since roads present structures with a greater ability to channel individuals towards the camera traps than game trails. However, trap placement on or off roads had a much stronger influence on jaguar than on puma detection. These results show that even for supposedly similar species detection probability itself and variation in detection probability can be quite distinct. In any analysis of camera trapping data these differences need to be taken into account.

Conclusion and conservation implications

Resource partitioning between sympatric pumas and jaguars most likely takes place at several levels of interaction. We showed that spatial avoidance of the dominant jaguar by the puma can take place in addition to any differences in habitat use. Pumas appear to be more opportunistic in their habitat use than jaguars and the predominantly open and dry ENP may seem more suitable to pumas than jaguars (Kelly et al., 2008). Although jaguar distribution within the park is wider than that of pumas, the species occurs at very low densities of 0.3-0.5 individuals 100km^{-2} (Chapter 2). Puma occurrence was more restricted within the park than that of jaguars. Pumas, however, are more tolerant of anthropogenic habitat alterations and have been regularly recorded beyond the park boundaries, whereas jaguars largely confine their movements to areas within the park boundaries (Silveira, 2004; Vynne et al., 2010). With the exception of a study by Foster et al. (2010) in Belize, this seems to be the general pattern (e.g., Leite and Galvão, 2002; Nuñez et al., 2002). The ability to focus on smaller prey should give the puma an advantage to persist in areas where large prey has been depleted (Haines, 2006).

In summary, the jaguar seems to be dominant over the puma and predominate where habitat conditions are favourable, i.e., in moister, more densely vegetated areas (Noss, 2006; Azevedo and Murray, 2007; Kelly et al., 2008). However, the small and confined jaguar population of ENP is likely to be much more susceptible to stochastic events than the park's puma population which is part of a larger regional population. As cultivated landscapes dominate most of the Cerrado, this situation is probably representative for other protected areas in this biome.

Acknowledgments

This study received financial support from the Disney Worldwide Conservation Fund, Fundação Monsanto, the Earthwatch Institute, the Memphis Zoo and the Leibniz Institute for Zoo and Wildlife Research. RS received a scholarship from the German Academic Exchange Service (DAAD). We thank ICMBio for granting permission to work in ENP and ENP management for logistical support. We are indebted to the entire Jaguar Conservation Fund team, all Earthwatch volunteers and interns, and especially Karlla Barbosa and Tiago Boscarato for their invaluable help with field work and picture analysis. We further thank Stephanie Kramer-Schadt for comments on an earlier draft of the manuscript.

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Supplementary material

WinBUGS run specifications and model code

WinBUGS uses Gibbs sampling, a Markov chain Monte Carlo (MCMC) method simulating samples from the joint posterior distribution of the unknown quantities in a statistical model (Casella and George, 1992). MCMC chains are started at arbitrary parameter values and since successive iterations depend on the outcome of the previous iteration, the start value will be reflected in a number of initial iterations that should be discarded (the burn-in). This characteristic can also lead to autocorrelation of successive iterations. To avoid autocorrelation, a thinning rate is specified as every i^{th} iteration used in the characterization of the posterior distribution of the parameters. We ran three MCMC chains with 5,000 iterations, a burn-in of 1,000 and a thinning rate of three. This combination of values ensured an adequate number of iterations to characterize the posterior distributions, that MCMC chains showed no indications of autocorrelation or effects of the initial values, and that all chains converged (i.e., oscillated around essentially the same mean parameter value). We checked for chain convergence using the Gelman-Rubin statistic (Gelman et al., 2004), R-hat, which compares between and within chain variation. R-hat values below 1.1 indicate convergence (Gelman and Hill, 2006). Values for all estimated parameters were below 1.1.

The WinBUGS model code, omitting the prediction of the rate of occupancy for grid cells, was:

```
model{

for (i in 1:nsites) {  #loop across all sites
r[i]<-roads[i]+1

#jaguar occupancy model
zJ[i]~dbern(psiJ[i])
lpsiJ[i]<-a+b*Dist[i]+c*Dense[i]+e[i]
psiJ[i]<-exp(lpsiJ[i])/(1+exp(lpsiJ[i]))
J[i]<-zJ[i]+1
ObsJ[i]~dbin(pJ[r[i], J[i]], Tx)     #Tx = number of repeated visits

#puma occupancy model
zP[i]~dbern(psiP[i])
lpsiP[i]<-aP+JagP*zJ[i]+bP*Dist[i]+cP*Dense[i]+eP[i]
psiP[i]<-exp(lpsiP[i])/(1+exp(lpsiP[i]))
P[i]<-zP[i]+1
ObsP[i]~dbin(pP[r[i],J[i],P[i]], Tx)
both[i]<-zJ[i]*zP[i]
}
```

```
#priors for jaguar occurrence model and detection probability conditional on occurrence
a ~ dflat()
b~dnorm(0, 0.1)
c~dnorm(0, 0.1)
for (j in 1:2){
pJ[j,1]<-0
px[j]~dunif(0,1)
pJ[j,2]<-px[j]
}

#priors for puma occurrence model and detection probability conditional on occurrence
aP~dflat()
bP~dnorm(0, 0.1)
cP~dnorm(0, 0.1)
JagP~dnorm(0,0.1)
pP[1,1,1]<-0
pP[2,1,1]<-0
pP[1,2,1]<-0
pP[2,2,1]<-0
pP[1,1,2]<-py
pP[2,1,2]<-pz
py~dunif(0,1)
pP[1,2,2]<-pP[1,1,2]
pP[2,2,2]<-pt
pz~dunif(0,1)
pt~dunif(0,1)

#Gaussian CAR priors for spatial random effects
e[1:nsites] ~ car.l1(adj[], weights[], num[], 0.75)
eP[1:nsites] ~ car.l1(adj[], weights[], num[], 0.75)
for (k in 1:sumNumNeigh) {weights[k] <- 1}

zJtot<-sum(zJ[])  #sites occupied by jaguars
zPtot<-sum(zP[])  #sites occupied by jaguars
btot<-sum(both[])  #sites occupied by both
Phi<-(btot/nsites)/((zJtot/nsites)*(zPtot/nsites))  #measure of spatial interaction
}
```

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CHAPTER 5

General discussion

The purpose of the present study was to collect basic information on the status of the jaguar population of Emas National Park, one of the last refuges for this and other large mammal species in the central Brazilian Cerrado grasslands. The study focused on estimating population abundance and density, baseline information for status assessment, and the investigation of foraging strategies, which gives cues about the prey base available to this large predator and key resources that need to be protected for its persistence. The study also looked into space partitioning between the jaguar and the sympatric puma. The second focus of the study was analytical-methodological, aiming to apply and develop novel approaches to handle small, sparse and incomplete data sets.

Methodological considerations – field methods

The present study applied three common field methodologies in carnivore research: camera trapping, scat collection and live capture for tagging individuals with GPS collars. Whilst camera trapping was successful and scat collection was successful to some extent, GPS-tagging yielded no actual data: In spite of a major effort, both with 30 cage traps deployed and checked daily for 6 months, and with trained tracking dogs, in 2009, we only captured a single male jaguar. The animal was fitted with a GPS collar manufactured by Telemetry Solutions, but the collar lost its GPS unit within three weeks (Figure 5.1). The collar automatically dropped off the animal a year later, but even from a plane we

Fig. 5.1: *Male jaguar with collar that has lost its GPS unit (arrow indicates where the GPS unit was located); picture taken by camera traps in Emas National Park.*

were unable to locate its VHF beacon, most likely due to failure, so no data points were obtained from this individual.

Unlike many other large mammals (Putman, 1984), jaguars defecate more frequently off than on roads (Vynne et al., 2010): of the 39 confirmed jaguar samples, only 9 were collected along park roads. In a situation such as here where scats have to be collected off road, the only applicable method for effective scat collection is the use of scat detector dogs with their ability to detect cryptic scats under or blending in with the vegetation. Even with using this advanced tool and pooling data from several years' effort, with 39 genetically confirmed jaguar scats sample size was still very small. Whereas the 2004-2008 effort comprised sampling for five mammalian species both within ENP and on farms in the surrounding area (Vynne et al., 2010), in 2009 we specifically targeted areas within the park where jaguars had been recorded. Vynne et al. (2010) estimated that dogs had an 88 % chance per visit of detecting jaguar faeces in quadrants known to be inhabited by jaguars. However, in 2009 average success remained low, with approximately 1 jaguar scat collected in every 33 km of transect.

In contrast, camera traps rendered over 100 records of 10 individual jaguars within 3 months. Although 10 individuals is still a small sample, particularly when considering the effect of sex on population parameters, in the light of the low population density this seems to represent most if not all adult individuals present in ENP. Inference based on camera-trapping data concerning the ENP jaguar population should therefore be reliable. Camera trapping also provided auxiliary information to study jaguar foraging behaviour and space partitioning between jaguars and sympatric pumas. Camera trapping proved therefore to be a very effective method to investigate a range of aspects of jaguar ecology, and more effective than even multi-year scat collection. This appears to contradict findings from earlier studies where scat detector dogs were more efficient in detecting carnivores than camera traps (Wasser et al., 2004; Long et al., 2007). However, while the number of detections per unit effort may be higher for scat detector dogs than for cameras in some instances, many simultaneously operational camera traps accumulate a larger amount of effort more rapidly. It is this characteristic that makes camera traps more suitable to investigate occurrence or population parameters of species occurring at very low densities. Of course, collection of faeces allows investigation of aspects other than occurrence and abundance, such as genetics, diet, hormone status, or diseases (Kohn and Wayne, 1997). Studies that intend to investigate these aspects in a very rare animal should consider the effort required to obtain a large enough sample to answer the specific research questions.

It has been argued that scat detector dogs, in working independent of fixed locations, as opposed to cameras and other fixed devices, should have less detection bias towards certain parts of the sampled population (Long et al., 2007). In the present setting, we would expect a lower bias towards males than that exhibited by camera traps. However, all scats that could be genetically sexed (11 out of 15 scats from the 2009 effort) stemmed from (at least three) males, so that at least in the present study, scat detector dogs seemed to have a detection bias towards males similar to or even stronger than that observed in the camera traps. Such biases towards parts of the sampled population can affect data interpretation. In the present case our interpretation of jaguar foraging ecology could be biased if prey preferences differed between males and females. The only study that investigated sex-specific differences in feeding behaviour noted a similar overall diet composition (Cavalcanti and Gese, 2010). Female jaguars are, on average, 10-20 % smaller than males (Seymour, 1989) and could therefore target smaller prey. Possibly, the overall lower movement rates of females and the need to provision for less mobile cubs could cause prey species with a higher degree of distributional overlap to be preferred. Only a larger sample with confirmed scats of females could give insight into these issues. Therefore, studies relying on scat detector dogs should not simply assume their tool to be unbiased but rather examine their potential sampling bias and account for it in analyses.

In conclusion, while camera trapping and scat collection yield complementary information, the former seems more effective for studying several aspects of ecology in animals occurring at very low population density. While scats can provide a range of valuable information, in very rare species the effort to collect an adequate number of samples to perform statistical analyses may be considerable, both logistically and financially. As scat detector dogs have repeatedly been advocated as the most effective method to study elusive carnivores (Wasser et al., 2004; Long et al., 2007), researchers should keep the limitations of this method in mind.

Methodological considerations – analytical approaches

The present study made extensive use of hierarchical models for data analysis. Hierarchical models have both conceptual and technical advantages (Royle and Dorazio, 2008). Conceptually, they force us to think about the different components of a studied system.

Technically, they account for sources of variation that arise from both the underlying ecological and the observation process, allow combination of data from different sources or collected at different scales (for example, landscape and site scale data; data from sampling over a short time period – say, months – which is repeated at larger time intervals – say, annually). Hierarchical models are also flexible and can be adjusted to accommodate different sampling situations or sources of variation in the parameter of interest (Royle and Gardner, in press).

For example, in chapter 2 we identified the assumption of circular home ranges as a drawback of the SECR model. Conceptually, we could readily lift this assumption and allow for elliptic home ranges, which may be more realistic for animals that orient their movement along linear landscape features, such as rivers in the case of ENP's jaguars. In addition to the latent individual home range centers we would have to estimate the ratio of the two axes of the ellipse (which could be constant for the population, differ with sex, by individual, etc.) and their spatial orientation, all latent parameters themselves. We would also have to adjust the movement model accordingly. The invocation of such a model requires a data set that is larger than available to the current study because of the increased number of parameters of interest. However, this example demonstrates the flexibility of the hierarchical SECR model in terms of considering species-specific, site-specific or sampling-specific characteristics, thereby improving insights into the spatial behaviour of a population.

The occupancy models applied in the present study all considered only a binary state variable (present or absent) for a single camera trapping season. Depending on the data at hand, these models can be expanded to multi-state models (e.g., absent, present but rare, present and abundant) or multi-season models to investigate occupancy dynamics (MacKenzie et al., 2006).

With their flexibility and ability to account for ecological and observation processes, hierarchical models are now an established approach in ecological research (Royle and Dorazio, 2008). Several standard analytical methods that also account for detection bias such as capture-recapture modelling can be formulated as hierarchical models (Royle and Dorazio, 2008). In the literature on large carnivores, however, many studies still base their conclusions on raw count statistics, which is the most error-prone approach when comparing species or sites. Recent examples include the comparative analysis of habitat use by jaguars and pumas (Foster et al., 2010), the differential use of roads and trails by forest mammals and resulting implications for camera trap sampling (Harmsen et al., 2009), or the comparison of prey consumed by jaguars with prey availability based on camera trap count statistics (Cavalcanti and Gese, 2010).

Hierarchical models are not a remedy to every problem. Particularly for the case when researchers are interested in the – absolute or relative – abundance of a species where individuals cannot be individually identified, there is no clear answer to the question of how to address the issue of detectability (for two separate, very distinct approaches, see Royle and Nichols, 2003 and Rowcliffe et al., 2008). In other cases, sample size may be too small to apply any statistical procedure. Even in these cases, the conceptual advantage of "thinking hierarchically" holds, namely, that it forces us to consider the different levels of the studied system and the processes involved in studying it. The consequences of this thought process should involve either the search for an alternative approach (e.g., using occupancy as a surrogate for abundance) or exploring the potential consequences of unaccounted detection bias on results and interpreting results accordingly.

As a side note, hierarchical model construction is independent of the mode of analysis and inference. Hierarchical models are often most conveniently analyzed in a Bayesian framework (Royle and Dorazio, 2008). In 'frequentist' analyses (see introduction), latent variables or random effects (for example, the true occupancy state in occupancy models) are removed from the model likelihood by integration. This approach does not work well for models with a complex structure of or dependencies among latent variables, such as in the SECR model (Royle and Dorazio, 2008; Royle and Gardner, in press). In Bayesian statistics, posterior distributions of all unknown quantities including latent variables are characterized with the help of Marcov chain Monte Carlo (MCMC) simulation methods. Within this framework, functions of latent variables can be formulated in an easy and coherent manner and a full account of all associated sources of uncertainty is possible (Royle and Dorazio, 2008).

In conclusion, hierarchical models analyzed in a Bayesian framework were the natural choice for most of the aspects analyzed in the present study and provided a wide range of opportunities to study aspects of large carnivore ecology that would have otherwise remained inaccessible.

Jaguar conservation status in the region of Emas National Park

ENP is the only large protected area in the southwest of the Cerrado (Figure 5.2) and thus a key element in the conservation of jaguars (and many other species) in this region. The park harbours a small, probably somewhat isolated population of jaguars. Jaguars concentrated their activity along the major water courses within the park and were estimated to occupy 54 % of the park area. In a regional context, occurrence of the species is almost entirely restricted to the park itself (Silveira, 2004), as opposed to other large carnivores such as pumas and maned wolves (*Chrysocyon brachyurus*), both occurring equally likely within and outside the park (Vynne et al., 2010). However, documented reproduction and the mere persistence of the species in the park over the past four decades indicate that the region holds some potential for the long-term persistence of the jaguar. Several factors contribute to this:

(1) The park harbours populations of several large mammal species, providing the jaguar with an abundant food source.

(2) Good park management and especially low human population pressure in the park's surroundings due to the system of large scale crop plantations lead to the absence of or very low poaching pressure on local wildlife and a low jaguar-livestock rancher conflict potential.

(3) Consequently, perception of the species is predominantly positive (Santos et al., 2008).

(4) Location of the Jaguar Conservation Fund's base in the immediate vicinity of the Park and the consequent direct contact between researchers and the local farm community contributes to awareness of the local population for conservation issues.

Still, the small population size and its relative isolation predispose the Emas jaguars to inbreeding depression and put them at risk of extinction by stochastic events, such as large fires. Fires are an integral part of the Cerrado ecosystem (Hoffmann and Moreira, 2002) but have to be managed in such a confined area as the national park to avoid serious damage to flora and fauna (Silveira et al., 1999). At the end of an extreme dry season, in August 2010, an out of control anthropogenic fire burnt over 80 % of the park area within 36 hours. Frosts that occur during dry season cause high foliage mortality, increasing the fuel load for late dry season fires (Silveira et al., 1999). Late dry season fires have been shown to develop higher temperatures and cause greater damage to soil and vegetation than early dry season fires in the Cerrado (Miranda et al., 2002) and other savanna ecosystems such as the Serengeti (Stronach, 1989) or the Madagascan savanna/dry forest habitat (Bloesch, 1999), attributed to a lower level of residual moisture in the soil and vegetation. While the park has undergone similar catastrophes before and dead individuals of several large mammal species have been reported after large fires (Silvera et al., 1999), we know very little about the effects of such events on animal populations, or how effects of successive events accumulate. Systematic long-term population monitoring with repeated camera trap studies could yield the data to investigate such effects on jaguar population dynamics and may have important implications for park fire management.

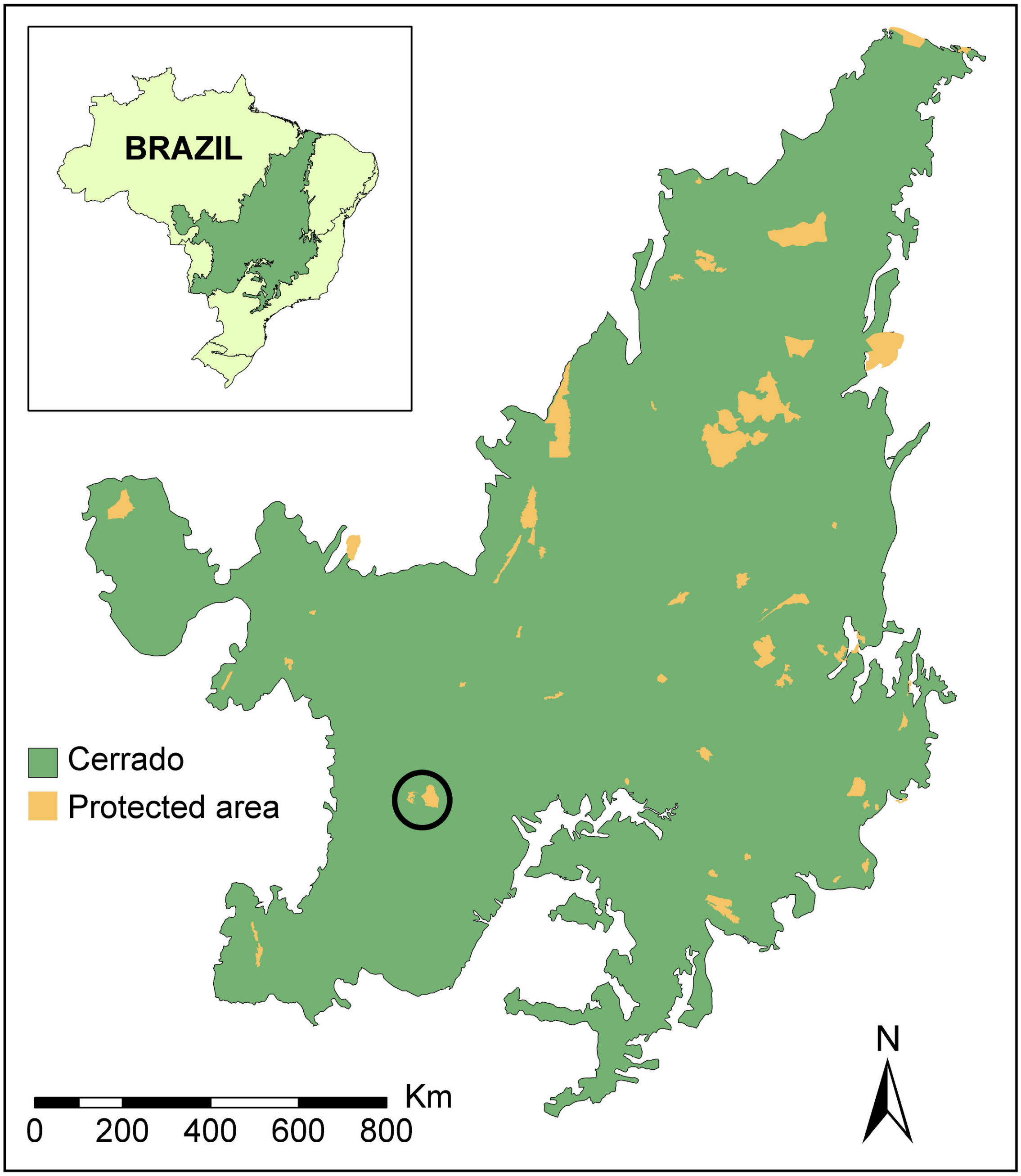

Fig. 5.2: *Protected areas above 100 km² in the Cerrado biome; the circle indicates the Emas National Park and the neighbouring Parque das Nascentes do Rio Taquari.*

In summary, although surrounded by mostly cultivated areas, the situation for the jaguar in ENP is still somewhat hopeful, although population size is very low and the surrounding agricultural areas have little potential to hold additional resident individuals. The species' status in the region therefore continues to be critical. Yet, some important aspects to fully assess the population status remain unknown: (1) Genetic diversity. The genetic diversity of the ENP jaguar population is currently being investigated. In the Atlantic Forest, Haag et al. (2010) found genetic evidence for a structure of isolated subpopulations of jaguars in a region where isolation of populations is thought to have happened within the last 30 years. We therefore would expect population isolation to show up in genetic markers despite the relatively recent physical isolation of ENP. (2) Actual degree of isolation. The degree of isolation of this jaguar population is currently being assessed. The basin of the Araguaia river, which has its source only 500 m beyond the park's north-western border and runs northwards through the Cerrado into the Amazon biome, passing 18 protected areas and indigenous reserves along its 2,000-km course, was identified by a JCF study as the most promising dispersal opportunity for jaguars in the region of ENP (JCF, unpublished data). The actual dispersal potential of this large scale corridor and the degree of connectedness among populations located along its course are also a focus of ongoing studies. Results will have important implications for the conservation status of the jaguar in ENP.

Implications for jaguar conservation in the Cerrado

Conservation of wide-ranging carnivores has largely shifted towards a landscape scale approach (Karanth and Chellam, 2009), recognizing that for many of these species reserves are not sufficient to hold viable populations and that the area that can be set aside for additional reserves is becoming increasingly limited (West et al., 2006). Still, in an ever changing and developing cultural landscape, protected areas continue to be one of the most important tools for conservation and should continue to be cornerstones for regional conservation planning (Noss et al., 1996; Margules and Pressey, 2000).

In an assessment of the potential of Brazilian protected areas to ensure the jaguar's long-term survival, Sollmann et al. (2008) identified 298 protected areas where the species occurred that theoretically were large enough to hold at least one breeding pair of jaguars. Of those, 60 areas (close to 20 %) were located in the Cerrado, second only to the Amazon biome. Yet, protected areas in the Cerrado were estimated to hold less than 5 % of all protected jaguars in Brazil because of their low average population size in this biome. Population size was then estimated on the basis of the only biome-specific density estimate available of 2 individuals 100km^{-2} (Silveira, 2004). The results from the present study suggest that these estimates were optimistic. If jaguar density in ENP was applied to other protected areas in the Cerrado, the entire biome would only hold some 350 protected jaguars, as opposed to the 2,300 estimated before. Although extrapolation from a single study site to an entire biome is of course associated with some uncertainty and density estimates are best interpreted in comparisons across biomes (Sollmann et al., 2008), this gives us an idea of the order of magnitude by which we may have overestimated jaguar abundance in the Cerrado before. Further evidence for low population densities come from the largest of the Cerrado national parks (Parque Nacional das Nascentes do Rio Parnaíba) where extremely low photographic rates of the species (1 in over 4,000 trap days; Lima, 2009) indicate that ENP may be at the higher end of jaguar densities in the Cerrado. Consequently, the existing protected areas alone are most unlikely to ensure jaguar persistence in the Cerrado (Sollmann et al., 2008). The lack of comprehensive knowledge about the distribution and status of the species in the Cerrado outside protected areas hampers a complete assessment of its conservation status in this biome.

Small protected populations would not represent so much of a conservation problem if they were embedded in larger regional population or interconnected with other populations. A set of interconnected populations (also termed meta-population) has an increased overall population size, protecting the species from negative effects of demographic, genetic and environmental stochasticity and allowing for re-colonization of extinct patches (Hanski, 1998; Hanski and Ovaskainen, 2000). Whereas about 60 % of the Cerrado is still covered by natural vegetation (MMA, 2007), 80 % is under some degree of human influence and the biome is characterized by a fragmented landscape (Cavalcanti and Joly, 2002). Large-scale crop plantations most likely present movement barriers or are at least extremely difficult dispersal habitat for jaguars (Rabinowitz and Zeller, 2010). Consequently, the major threat to the species in the Cerrado is the isolation of populations too small to be viable over the long term (Silveira and Jácomo, 2002).

Corridors that link populations and provide individuals with dispersal opportunities have been proposed as a tool to achieve landscape and population connectivity (Chetkiewicz et al., 2006). The Brazilian environmental legislation that requires land owners to protect parts of their property for biodiversity conservation provides a starting point for the implementation of such corridors. While we know little about jaguar occurrence outside of protected areas in the Cerrado, we assume that it will coincide with a less intensive human use of the landscape, which in turn generally coincides with cattle ranching. Therefore, we should expect a high potential for jaguar-livestock rancher conflict. Conservation efforts for the Cerrado jaguars should primarily tackle the issue of habitat connectivity, both on a local and larger scale, and simultaneously address the potential for human-jaguar conflict.

Implications for future jaguar research in ENP and the Cerrado

The establishment or maintenance of landscape connectivity to avoid isolation of small populations is probably the most pressing issue for jaguar conservation in the region of ENP and the Cerrado in general. The range-wide assessment of landscape potential for jaguar dispersal by Rabinowitz and Zeller (2010), assigning dispersal costs to vegetation cover types based on expert opinion, provides a valuable coarse scale assessment of where to look for suitable structures to establish or protect potential dispersal corridors. In addition, the practical implementation of a corridor also needs to be evaluated on different spatial scales – local, regional and on the level of biome. Against this background, I propose three major areas of applied jaguar research for the Cerrado:

(1) As the jaguar's ability to use the fragmented Cerrado landscape remains unknown, the concept of functional habitat connectivity for jaguars is speculative. Movement of such mobile species as the jaguar is most effectively studied by GPS-based telemetry. In spite of the associated difficulties and risks (Furtado et al., 2008), if efforts are well planned and are undertaken by an experienced team and with fully functional equipment, data from areas like ENP have the potential to be extremely valuable for conservation efforts of the species in the Cerrado. In spite of the low capture success in ENP in 2009, the efforts to GPS-tag jaguars should be continued, both in ENP and in other non-protected study areas of the Cerrado.

(2) On a larger scale, the occurrence of the jaguar throughout the Cerrado needs to be investigated in order to identify existing populations outside protected areas and understand which environmental characteristics favour or discourage the occurrence of the species. This assessment will allow the identification of key jaguar populations that are unprotected and of those areas that have dispersal potential on an intermediate and a biome scale.

(3) In areas holding unprotected key populations or deemed to have a high potential for jaguar dispersal, presence and intensity of the jaguar-livestock rancher conflict and the general attitude towards the species need to be evaluated to address the socio-cultural potential for jaguar conservation.

Related ongoing jaguar research projects

The present study is part of a larger institutional program by the JCF to investigate jaguar ecology and conservation status in the Cerrado. Specifically in ENP, camera trapping will be continued to investigate jaguar population dynamics using open population capture-recapture models as described by Karanth et al. (2006) in a non-spatial approach and by Gardner et al. (in press) and Royle and Gardner (in press) using spatially explicit capture-recapture models. Scats collected in the present study are part of several collaborative projects concerning jaguar genetics (Estación Biológica de Doñana, Spain), or the comparative feeding ecology of jaguars and pumas (Carly Vynne, University of Washington, and Julie Betsch, University of Montana), and part of an on-going Ph.D. thesis on jaguar epidemiology (Mariana M. Furtado, JCF and University of São Paulo).

ENP is also embedded in a larger project to protect the course of the Araguaia river as a potential biodiversity corridor for central Brazil. The 2,000-km course of the Araguaia river provide an important refuge for central Brazil’s biodiversity, apart from an important potential dispersal corridor for the jaguar, one of the project’s focal species. The project is carried out in close collaboration with government authorities and local landowners. Thus, insights gained in the present study contribute to a series of multi-disciplinary investigations on a larger scale on jaguar biology, ecology and conservation.

Conclusions

Owing to the low population density, camera trapping was the most effective methodology to study jaguars in ENP. The method yielded large amounts of non-target species data that could be used to investigate aspects of foraging ecology and spatial interactions with the sympatric puma. Hierarchical models, implemented in a Bayesian framework, proved ideally suited for the analysis of the data.

ENP holds one of the last protected populations of jaguars and pumas in the Cerrado. Both species have persisted in ENP in spite of the rapid and large-scale conversion of the region to cultivation over the last five decades. The park seems to accommodate an abundant prey base for both predators. However, the low population size and high degree of isolation make the local jaguar population vulnerable to extinction. The puma’s distribution within the park is restricted by the occurrence of the competitively dominant jaguar. Yet the local situation of the puma is probably more stable, as pumas are also found in the surrounding agricultural areas so that the park’s population is embedded within a larger regional metapopulation. For many other protected areas in the Cerrado biome, the situation is probably similar. Conservation efforts for the jaguar should focus on landscape connectivity to ameliorate the effects of small population size and isolation. Consequently, research should address questions of where unprotected jaguar populations are found in the biome and how the species could use and move through the anthropogenically altered landscape of the Cerrado.

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SUMMARY

The jaguar *Panthera onca* is the largest felid of the Americas and threatened by habitat loss and direct conflict with humans. Owing to low population densities and cryptic habits it remains little studied, especially in the central Brazilian Cerrado grassland. The present dissertation investigated population status and ecology of the jaguar in Emas National Park (ENP), one of the most important Cerrado reserves.

Abundance and density is baseline information for conservation planning. In chapter 2, I estimated jaguar density based on data from a park-wide camera trapping study using regular and spatially explicit capture-recapture models. I observed 10 adult individuals and estimated a density of 0.3-0.6 individuals 100km^{-2}. The spatially explicit approach accounts for animal movement on and off the trapping grid in a formal way and is therefore preferable over the non-spatial approach. Due to the considerable degree of isolation, the small size of the ENP jaguar population exposes it to a risk of extinction by stochastic factors.

Since predator ecology is largely governed by their prey, understanding a predator's foraging ecology can contribute to its conservation. In chapter 3, I analyzed jaguar feeding ecology based on scats collected with the aid of scat detector dogs. Despite a large effort, we only obtained 39 genetically identified jaguar scats. Since the sample was ill-suited for standard analyses, I measured prey availability based on distributional overlap with the predator derived from occupancy models to investigate selection. I further developed a qualitative optimal foraging model assessing expected foraging costs and benefits to predict prey preferences. Giant anteaters had the second lowest distributional overlap with jaguars but accounted for 75 % of its diet, indicating selection. The model predicted giant anteaters to be the most profitable prey, suggesting that selecting for them is the optimal foraging strategy for jaguars in ENP.

Resource partitioning is a mechanism fostering co-existence. In chapter 4, I investigated space partitioning between jaguars and pumas in ENP using camera trapping data and occupancy models that account for imperfect species detection and spatial autocorrelation. Jaguar occurrence was positively correlated with the amount of dense habitat in the trap area and negatively correlated with the distance to water. Puma occurrence was negatively correlated with jaguar presence. Both species occurred less often together than expected under independent distributions. Jaguars used more of ENP than pumas. The more generalist puma is frequently found beyond the park boundaries, whereas jaguars are largely restricted to the park. Though outcompeted by the jaguar within the park, the conservation situation of the puma is less worrying than of the isolated small jaguar population.

Overall, camera trapping proved more efficient than scat collection to study jaguar ecology in ENP because of the low population density and the ability of camera traps to simultaneously accumulate a larger amount of effort. Hierarchical models are flexible to suit specific sampling and data situations and explicitly account for the observation process, and are thus ideal to investigate carnivore ecology. Jaguar conservation in ENP and the Cerrado should focus on the issue of small population isolation and the potential for dispersal corridors. In the same context, research should focus on the identification of remaining Cerrado jaguar populations and landscape use of jaguars outside of protected areas.

ZUSAMMENFASSUNG

Der Jaguar *Panthera onca*, die größte Katze Amerikas, ist bedroht durch Habitatzerstörung und Konflikte mit Menschen. Seine geringe Dichte und versteckte Lebensweise führen dazu, dass die Art relativ unerforscht ist, besonders in der zentralbrasilianischen Cerrado Savanne. Die vorliegende Arbeit befasst sich mit dem Populationsstatus und der Ökologie des Jaguars im Emas Nationalpark (ENP), einem der wichtigsten Cerrado-Reservate.

Abundanz und Dichte sind grundlegende Informationen für den Artenschutz. In Kapitel 2 schätzte ich die Jaguardichte im ENP, basierend auf Kamerafallen-Daten, mithilfe von regulären und räumlich expliziten Fang-Wiederfang-Modellen. Ich photographierte 10 Individuen und schätzte die Dichte auf 0.3-0.6 Individuen $100km^{-2}$. Das räumlich explizite Modell berücksichtigt Bewegungen vom und ins Studiengebiet formell und ist daher den nicht-räumlichen Modellen vorzuziehen. Da sie sehr klein und weitgehend isoliert ist, besteht für die ENP-Jaguarpopulation das Risiko der Ausrottung durch stochastische Prozesse.

Da Raubtierökologie weitgehend durch die Beute bestimmt wird, tragen Kenntnisse über die Nahrungsökologie eines Raubtiers zu seinem Schutz bei. Im 3. Kapitel analysierte ich die Nahrungsökologie des Jaguars basierend auf Kot, der mithilfe von Kotspürhunden gesammelt wurde. Trotz großen Aufwands fanden wir nur 39 Proben, die genetisch als vom Jaguar identifiziert wurden; daher waren statistische Standardanalysen nicht anwendbar. Mithilfe von Vorkommensmodellen schätzte ich die räumliche Überlappung zwischen Jaguar und Beute als ein Maß für Beuteverfügbarkeit, um auf Selektion zu testen, und entwickelte ein qualitatives, optimales Nahrungssuchmodell, indem ich erwartete Kosten und Nutzen gegeneinander abwog, um Beutepräferenz vorherzusagen. Trotz zweitgeringster räumlicher Überlappung machte der große Ameisenbär 75 % der Jaguarnahrung aus. Das Modell sagte voraus, dass große Ameisenbären die profitabelste Beute seien. Die Selektion von Ameisenbären scheint die optimale Nahrungssuch-Strategie für Jaguare im ENP zu sein.

Die Aufteilung von Ressourcen fördert das Zusammenleben von Arten. In Kapitel 4 untersuche ich die Raumaufteilung zwischen Jaguaren und Pumas mithilfe von Vorkommensmodellen, die imperfekte Detektierung und räumliche Autokorrelation berücksichtigen. Das Vorkommen von Jaguaren war positiv korreliert mit dem Anteil an dichtem Habitat in der Kamera-Umgebung und negativ korreliert mit der Distanz zu Wasser. Das Vorkommen von Pumas war negativ korreliert mit dem Vorkommen von Jaguaren. Beide

Arten kamen weniger häufig zusammen vor als unter unabhängigem Vorkommen erwartet. Jaguare nutzten mehr vom ENP als Pumas. Pumas kommen häufig außerhalb der Parkgrenzen vor, während Jaguare sich weitgehend auf den Park beschränken. Daher ist die Situation für den Puma im ENP weniger prekär als für die isolierte kleine Jaguarpopulation, obwohl der Jaguar innerhalb des Parks die dominante Art zu sein scheint.

Insgesamt waren Kamerafallen effektiver als Kotsuche, um die Ökologie von Jaguaren im ENP zu untersuchen. Dies liegt an der geringen Jaguardichte und der Tatsache, dass Kameras simultan mehr Aufwand akkumulieren. Hierarchische Modelle sind flexibel, um speziellen Feld- und Datensituationen angepasst zu werden und berücksichtigen imperfekte Detektierung. Sie sind daher ideal für die Untersuchung von Raubtierökologie. Jaguarschutz im ENP und dem Cerrado sollte sich auf die Möglichkeiten konzentrieren, kleine Populationen mit Verbreitungskorridoren zu vernetzen. Parallel sollte sich die Forschung darauf konzentrieren, die übrigen Jaguarpopulationen des Cerrado zu identifizieren und die Nutzung von ungeschütztem Habitat durch Jaguare zu untersuchen.

ACKNOWLEDGMENTS

This thesis would not have been possible without the Jaguar Conservation Fund / Instituto Onça-Pintada, whose founders, Dr. Leandro Silveira and Dr. Anah T.A. Jácomo, initiated the jaguar project in Emas National Park (among many other initiatives) and created the entire foundation of logistics, contacts, licenses etc. that makes jaguar research in Emas National Park possible. Welcoming me into their team, Anah and Leandro gave me an opportunity way beyond the realization of a dissertation – they opened a door for me to step into the complex world of conservation. I also thank them for their kind hospitality throughout all my time in ENP.

My special thanks go to Mariana Malzoni Furtado and Natália Mundim Tôrres. They supported me in innumerous ways throughout my time in Brazil – housing me, driving me around, helping me with bureaucratic issues. Their comments and suggestions at all stages of work involved in the present project contributed largely to the success of this thesis. They also became great friends and I hope they both know how much it means to me to have been welcomed so warmly into their lives. I particularly thank Mariana, who was my first person of confidence within the JCF, for her continuing friendship and support. I consider her one of my closest – though farthest away – friends.

My gratitude extends to the entire JCF team and some former members, who have become my colleagues and friends, and without whose help I would never have been able to carry out the work associated with this project: Raphael Almeida, Samuel Astete, Fabiano Bortolini, James Bortolini, Tiago Boscarato, Eliot Cohen, Luana Delgado, Eduardo Freitas, Guilherme Lana, Darivan Nogueira, Grasiela Porfírio, Flávia Santos, Nuno Negrões Soares, Marina Zanin.

The project received help from many interns and Earthwatch volunteers, but I especially thank Karlla Barbosa and Felipe Vitaliano, for they were much more than "just interns" passing though.

Of course, the German counterpart of this thesis has been equally important for its success. Particularly, I thank Prof. Dr. Heribert Hofer for accepting me as a doctoral student after having known me for 30 minutes. I thank him for the interesting and fruitful discussions about the content of this thesis, as well as for arranging for the IZW to support me financially throughout large parts of the time I spent in Berlin.

Furthermore, I thank Prof. Hofer and Prof. Kipper for the kind evaluation of the present thesis.

Many thanks go to my IZW colleagues (and their partners), who, although I spent most of my time away from Berlin, always welcomed me back into their group whenever I was here. I thank Jan Axtner, Niko Balkenhol, Aines Castro Prieto, Simon Ghanem, Stephanie Kramer-Schadt, Camila Mazzoni, Mirjam Nadjafzadeh, Kathleen Röllig, Pablo Santos, Friederike Scholz and Justine Sulawa. Special thanks go to Andreas Wilting, who also arranged for me a source of income when I most needed one. Mirjam, Friederike and Andreas also helped improve this thesis with valuable comments and critique.

I thank the German Academic Exchange Service (DAAD) for the two years of scholarship that allowed me to do my field work in Brazil, as well as for two travel grants, to the Mammalogical Congress in Mendoza and to the USGS Patuxent Wildlife Research Center.

At Patuxent I thank Dr. James D. Nichols for his advice with several capture-recapture analyses, James E. Hines for the computational help with MARK, and Dr. J. Andy Royle for his advice on spatially explicit capture-recapture modelling and ideas for further data analyses. I am particularly indebted to Dr. Beth Gardner, who guided me through the spatial capture-recapture model analysis, made numerous valuable suggestions concerning the respective manuscript and its submission, and has been a constant source of advice, suggestions and help on other topics ever since.

Last but certainly not least there is my incredibly strong system of support, wise life advisory council and unbreakable safety net that got me through all the rough patches along the way of this thesis: Thanks to my wonderful family Holdi Sollmann, Clemens Knobloch, Nana Sollmann, Rosalie und Lu Sollmann Maerker, Michel Maerker; to my much-more-than-just-a-boyfriend boyfriend Oliver OJ Jäger; and my closest friends Pia Kulozik, Lisa Sollmann, and Vera Warmuth.

The field work of the thesis has been financially supported by the Fundação Monsanto, the Earthwatch Institute, the Disney Worldwide Conservation Fund, the Memphis Zoo, and Idea Wild.