Original Investigation

Using occupancy models to investigate space partitioning between two sympatric large predators, the jaguar and puma in central Brazil

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ABSTRACT

Coexistence of sympatric species is mediated by resource partitioning. Pumas occur sympatrically with jaguars throughout most of the jaguar's range but few studies have investigated space partitioning between both species. Here, camera trapping and occupancy models accounting for imperfect detection were employed in a Bayesian framework to investigate space partitioning between the jaguar and puma in Emas National Park (ENP), central Brazil. Jaguars were estimated to occupy 54.1% and pumas 39.3% of the sample sites. Jaguar occupancy was negatively correlated with distance to water and positively correlated with the amount of dense habitat surrounding the camera trap. Puma occupancy only showed a weak negative correlation with distance to water and with jaguar presence. Both species were less often present at the same site than expected under independent distributions. Jaguars had a significantly higher detection probability at cameras on roads than at off-road locations. For pumas, detection was similar on and off-road. Results indicate that both differences in habitat use and active avoidance shape space partitioning between jaguars and pumas in ENP. Considering its size, the jaguar is likely the competitively dominant of the two species. Owing to its habitat preferences, suitable jaguar habitat outside the park is probably sparse. Consequently, the jaguar population is likely largely confined to the park, while the puma population is known to extend into ENP's surroundings.

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) and 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, 1991). Several authors report avoidance between jaguars and 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). In a larger spatial context, pumas seem to be rare at sites where jaguars are abundant (Rabinowitz and Nottingham, 1986; Azevedo and Murray, 2007) and vice versa (Noss et al., 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. While aspects

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of spatial ecology and interaction among species and/or individuals are best studied using radio or GPS-based telemetry (Millspaugh and Marzluff, 2001), these methodologies are invasive and for elusive species like jaguars often have to rely on small sample size. In contrast, non-invasive methods such as camera traps can yield information on a larger part of the population under study (MacKay et al., 2008). Since camera detections can be geographically referenced, these data can also be used to gain insight in aspects of spatial ecology of elusive species (Kays and Slauson, 2008; Harmsen et al., 2009; Foster et al., 2010).

However, just as with other survey methods, our ability to detect a species present in an area with a camera trap is not perfect. Whether or not (or how often) we detect a given species will depend on how it moves through the area we sample and where and how we set up the camera trap. Therefore, the use of raw photographic data such as count statistics can be problematic. Analyses of space use can lead to biased results if they do not account for imperfect detection, which can further vary among species and in space (MacKenzie et al., 2006; Royle and Dorazio, 2008). An adequate approach to this problem is provided by hierarchical models, which explicitly describe the observation process–in this case detection by camera traps – separately from the underlying ecological process–here, the actual distribution of a species in space (Royle and Dorazio, 2008). In the present study 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.

Material and methods

Study site

Emas National Park, listed as a Human Heritage Reserve by UNESCO, is located in south-western Goiás state (18°19′S, 52°45′W; Fig. 1) in the Cerrado grasslands of central Brazil. The park has a size of 1320 km² and protects large tracts of grassland plains, interspersed with small patches of shrub fields, marshes, and riparian forest. During the wet season (October–March), rainfall averages 1500 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 covering the entire ENP (Fig. 1) to estimate jaguar abundance and density in the study area (Sollmann et al., 2011). Distances between neighbouring stations were approximately 3.5 km, following recommendations for abundance estimation in jaguars (Silver, 2004). Cameras were predominately set along park roads; at off-road locations, we installed cameras along game trails. For unequivocal individual identification, each station consisted of two camera traps of 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. During approximately 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 24 h day^{-1} in shady locations and only during night time in exposed locations. To avoid bias, we only used photographs taken at night for our analysis. We are confident that this choice did not influence our analysis as in ENP radio-telemetry showed that both species are predominantly nocturnal (Silveira 2004). An analysis of records from camera traps working 24 h day^{-1} confirmed this observation (data not shown).

Occupancy model

Occupancy models estimate the probability of a species occupying a sampling site while correcting for imperfect species detection based on repeated detection/non-detection data (MacKenzie et al., 2006). They 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: $O_i \sim$ Bernoulli (Ψ).

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 are used to estimate detection probability p conditional on occupancy. 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).

Implementation of the model in a Bayesian framework explicitly estimates the partially latent O, is straightforward and allows the definition of functions of the estimated occupancy state (MacKenzie et al., 2006; Royle and Dorazio, 2008). Thus, this approach enabled us to estimate the number of sites occupied by jaguars (J), pumas (P) and both species (B) as

$$J = \sum O_J; P = \sum O_P; B = \sum (O_J \times O_P)$$

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 $\varphi = \Psi$(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 estimated to be 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

$$\varphi = \frac{B_r}{J_r \times P_r}$$

Single-season occupancy models 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
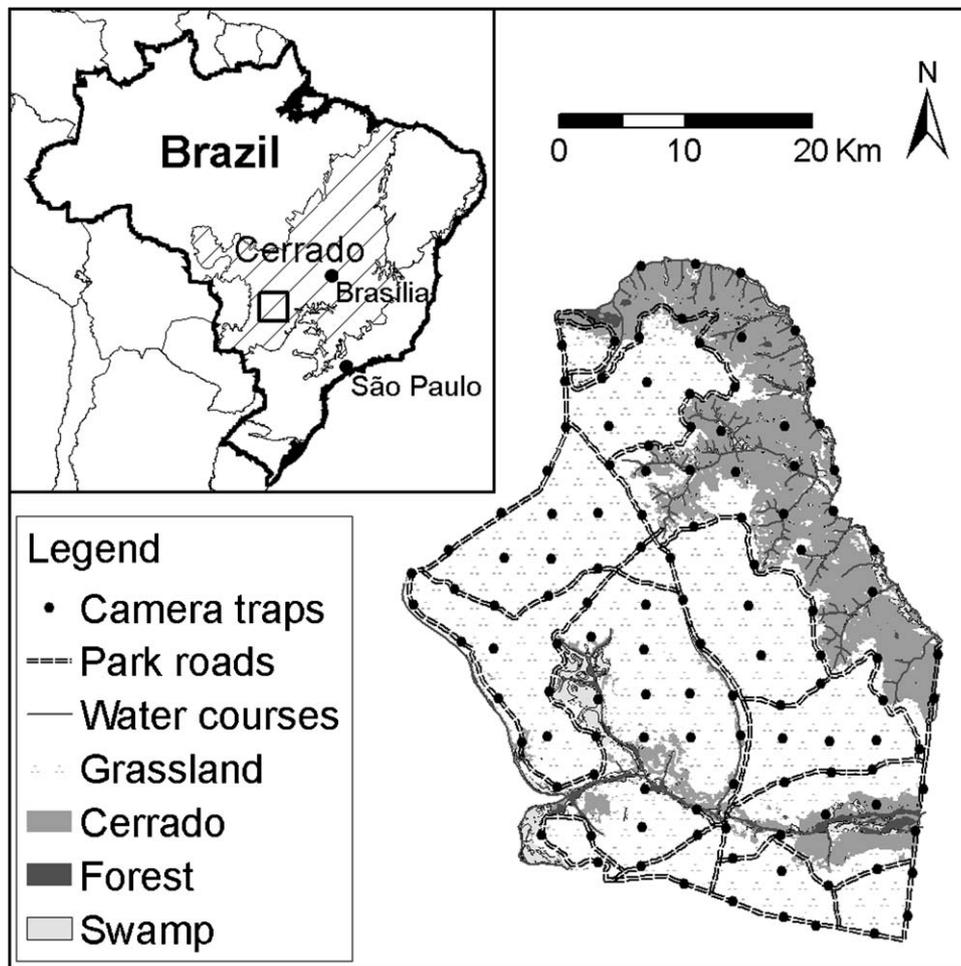
Fig. 1. Camera trap setup in Emas National Park; the square in the inset map marks the location of the study area within Brazil.

camera trap. Therefore, we divided our camera trapping period into five consecutive 16-day 'occasions' 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. For each trap site and each occasion we noted whether the species had been photographed or not.

We separately modelled both jaguar and puma occupancy 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 open grasslands and swamps) in a 1750-m buffer around the camera trap. This corresponded to half the average distance between neighbouring traps. As 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. We derived both measures from available GIS data of the park. The park's system of water courses is composed of the headwaters of two streams and their tributaries, which are adequately represented in the GIS layer. For pumas, we added the jaguar occupancy state O_J as a binary covariate. Owing to our sampling design and the mobility of the studied species, occupancy states could be spatially autocorrelated, i.e., the state of occupancy at a given site could be influenced by the occupancy state of a site nearby. To account for possible spatial autocorrelation, we added a random spatial effect e to the linear predictor of logit(Ψ). Its value at site i, e_i, is conditional on the value of e at all sites in the neighbourhood, corresponding to a conditional

autoregressive (CAR) model (Besag et al., 1991). We defined the neighborhood of each sampling site as all camera traps within a certain radius.

We ran CAR models for neighborhood radii ranging from 4 km (including only the closest neighbouring cameras) to 52 km (including all other cameras) and tested for spatial autocorrelation in model residuals calculated following Moore and Swihart (2005) using Moran's I (Cliff and Ord, 1973). The smallest neighborhood radius where we found no evidence of spatial autocorrelation in model residuals was 7 km. We therefore adopted this value for our final CAR model and concluded that this approach was sufficient to correct for the actual spatial autocorrelation in the data. For both species we modelled detection probabilities p_J and p_P as functions of camera trap placement on or off road (r, a binary vector of 1 for on-road locations and 0 otherwise). For pumas, we further included O_J as a possible covariate on 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 – BCI95) of the posterior distributions of the estimates. The model code and run specifications can be found in the supplementary material.

Results

During the five sampling occasions we obtained a total of 75 jaguar detections at 37 (31.1%) of the 119 sample sites and 49 puma detections at 32 (26.89%) of the sample sites. Jaguar detections corresponded to ten individuals (five males and five females, Sollmann et al., 2011). While pumas could not be individually identified based on our photographs, Silveira (2004) estimates pumas to be more abundant that jaguars in ENP, so that we believe that our puma detections correspond to at least as many individuals. We detected both species together at nine (7.6%) sample sites. The number of sites estimated to be occupied was $64.3 \pm SE 4.7$ (54.1%) for jaguars, $46.8 \pm SE 7.5$ (39.3%) for pumas and $18.6 \pm SE 5.1$ (15.6%) for both species together. The degree of spatial interaction between jaguars and pumas, φ, was $0.73 \pm SE 0.13$ (BCI95: 0.51–0.99).

Jaguar occurrence was negatively correlated with distance to water and positively correlated with the percentage of dense habitat (Table 1). Puma occurrence showed a weak negative correlation with jaguar occurrence and with distance to water, and no evident correlation with percentage of dense habitat (Table 1).

Jaguar detection probability was significantly lower at off-road locations ($0.05 \pm SE 0.02$) than at on-road locations ($0.37 \pm SE 0.04$). For pumas, detection was lowest off road ($0.19 \pm SE 0.08$), followed by on-road locations without jaguar presence ($0.23 \pm SE 0.05$) and with jaguar presence ($0.27 \pm SE 0.08$). Considering the overlap of the BCI95 of all estimates, the differences in puma detection probabilities across locations were not significant.

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 30% of the jaguar's distribution was occupied by pumas), the investigated habitat characteristics affected their occurrence in different ways. Jaguar occurrence increased significantly 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, showing only a weak negative correlation of puma occurrence with distance to water and no correlation with the amount of dense habitat (Table 1). Pumas are thought to be super generalists in their food and space use habits (Iriarte et al., 1990) and 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 (Núñez et al., 2000; Polisar et al., 2003). However, overall habitat use by both cats is often similar where sympatric (Schaller and Crawshaw, 1980; Taber et al. 1997; Scognamillo et al., 2003; Hernández, 2008; Harmsen et al., 2009; Foster et al., 2010).

In addition to differences in habitat associations between pumas and jaguars, we also investigated whether the estimated presence of jaguars had an effect on puma presence. We did observe a negative, albeit weak, correlation of puma occurrence with jaguar presence (Table 1). While the 95% BCI included 0, most of the density of the posterior distribution of the parameter was located below 0 (Table 1). Since we also accounted for differences in habitat use by both species in our analyses, this indicated some degree of

active spatial avoidance between jaguars and pumas. This is further corroborated by the measure of spatial interaction of both species, φ: With a value of 0.73 φ was well below 1, the value expected if the distributions of both species were independent of each other. Although our approach does not permit any conclusion about whether pumas avoided jaguars or vice versa, we believe the former scenario to be more likely: In the study area jaguars weigh on average close to 90 kg, while male pumas only attain about half that mass (Silveira, 2004).

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, 1987; Núñez et al., 2000; Leite and Galvão, 2002; Scognamillo et al., 2003). Our results suggest that the partitioning of food resources between both species could be influenced by their partitioning of space and by habitat preferences of prey species of common interest to both predators. Although rarely considered by studies of jaguar and puma feeding ecology (but see Weckel et al., 2006 for jaguars), the spatial distribution of the prey in relation to the predator is crucial to determine prey availability (Kruuk, 1986; Sunquist and Sunquist, 1989). Considering the spatial distribution of predators and prey in future comparative diet studies of jaguars and pumas could enlarge our understanding of resource partitioning between these two species.

Few authors found strong evidence for temporal segregation between jaguars and pumas 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 and jaguars avoided each other 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. While 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.

Methodological considerations

By applying the Bayesian formulation of a two-species occupancy model, we investigated habitat associations and the pattern of co-occurrence of jaguars and pumas in ENP while simultaneously accounting for imperfect species detection. It is intuitive that ignoring imperfect detection would lead to an underestimate of the area occupied by the species of interest, in the present case by 42% for the jaguar and 32% for the puma. But detection also varied spatially and between species. Both species were more readily detected at on-road locations than off-road. This is expected, particularly in the open habitats that dominate in ENP, since roads present structures with a greater ability to channel individuals towards the camera traps than game trails. But while for jaguars the difference in detection probabilities was strong, for pumas the difference was not significant. Further, at on-road locations the detection probability was slightly lower for pumas than for jaguars, but off-road, pumas had a significantly higher detection probability than jaguars. These results show that even for supposedly similar species like two large cats, detection probability itself and variation of detection probability (with trap placement in the present case, or with other variables not investigated here such as time or study site) can be quite distinct. If such differences are not considered in the analysis of camera trapping data – for example when using uncorrected count statistics – results will likely exhibit complex bias and

Table 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 1750-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)	−2.63	−1.42	−0.57
	$\beta(Dense)$	1.35 (0.77)	0.04	1.28	3.09
	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	$\beta(Dist)$	−0.28 (0.42)	−1.10	−0.28	0.54
	$\beta(Dense)$	−0.15 (0.36)	−0.91	0.09	0.55
	$\beta(O_J)$	−1.19 (0.86)	−2.96	−1.17	0.41
	p (off road)	0.19 (0.08)	0.08	0.18	0.37
	p (on road, $O_J = 0$)	0.23 (0.05)	0.14	0.22	0.34
	p (on road, $O_J = 1$)	0.27 (0.08)	0.13	0.26	0.43

may lead to erroneous conclusions about habitat associations and patterns of co-occurrence of the investigated species.

Conclusion and conservation implications

We showed that spatial avoidance between jaguars and pumas 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). However, jaguar distribution within the park was wider than that of pumas, possibly because the larger jaguar is the competitively dominant species. Nevertheless, jaguar density in ENP is very low, 0.3–0.6 individuals 100 km^{-2} (Sollmann et al., 2011). In addition, the surroundings of ENP are dominated by open agricultural landscapes: 44% of the park's surrounding is covered by crop plantation and 25% by cattle pasture; the 31% remaining natural vegetation are very fragmented (Vynne et al., 2010). Considering their association with dense vegetation and water, suitable jaguar habitat is thus likely very restricted outside of ENP. As a consequence, the park harbours a small and largely isolated jaguar population. In contrast, the generalist pumas have been shown more tolerant of anthropogenic habitat alterations (Leite and Galvão, 2002; Núñez et al., 2000). Specifically in the study region, Vynne et al. (2010) found pumas to be as likely to occur outside the park as inside: the species even occurred more than 20 km away from the park border. Silveira (2004) reports that for several radio-collared pumas large parts of their home ranges were located outside the park. Both studies show that in contrast, evidence of jaguars was virtually confined to within the park. Thus, the pumas of ENP seem to be part of a larger regional population and therefore less vulnerable to the negative effects of isolation than the jaguar. As cultivated landscapes dominate most of the Cerrado, this situation is probably representative for other protected areas in this biome.

Acknowledgements

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.mambio.2011.06.011.

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