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Occurrence of top carnivores in relation to land protection status, human settlements and rock outcrops in the high mountains of central Argentina

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ABSTRACT

We evaluated puma (*Puma concolor*) and culpeo fox (*Pseudalopex culpaeus smithersi*) occurrence in relation to a national park where livestock was reduced and hunting banned, and in relation to human presence and landscape features. In the high mountains of central Argentina puma signs were about 3.5 times less frequent than culpeo signs. Puma and culpeo signs were 33 and 19 times, respectively, more abundant within than outside the park. Puma signs increased with distance to settlements within the park but no trend was detected outside the park where signs were scarce. Culpeos were abundant all throughout the park with no relation with distance to settlements while outside the park signs increased with distance from settlements. Rock outcrops had a positive effect on pumas, which used this habitat frequently, and negative effect on culpeos, whose presence decreased slightly at sites with the highest proportion of rock outcrops inside the park and sharply at sites with presence of rock outcrops outside the park. We conclude that top carnivores were positively affected by the park creation and encourage the creation of more protected areas with connectivity in the region to better assure the long-term conservation of top predators.

1. Introduction

Landscape transformations due to the expansion of agriculture and urbanization are the most serious threats to biological conservation (Blaum et al., 2007; Fleischner, 1994; Hayward et al., 1997), particularly to terrestrial top carnivores (Crooks, 2002; Novaro and Walker, 2005). Habitat fragmentation is a clear example of the negative effect of human activities on top carnivores (Blaum et al., 2007; De Angelo et al., 2011; Logan and Sweanor, 2001; Mladenoff et al., 1995). Top carnivores usually respond to complex and interdependent environmental variables, the identification of which is not straightforward; however, those variables are important to understand the occurrence of carnivores and the effects of human intervention (Hirzel and Le Lay, 2008; Riley and Malecki, 2001).

Several studies have examined the complexity and interdependency of factors affecting top predators. For some carnivores, roads play antagonistic roles, being positive when they function as corridors or sources of prey (Fuller et al., 1992; Mladenoff et al., 1995; Ramp et al., 2006; Theil, 1985) or negative when they are highly travelled and easily accessible to humans (Dickson et al., 2005; Mech, 1989; Thurber et al., 1994). Studies of movement of pumas (*Puma concolor*) show their aversion to paved roads and human-modified vegetation types, and no aversion to dirt roads (Dickson and Beier, 2007). Topography and vegetation also have a critical effect on habitat use and dispersal of pumas in North America and are important landscape components for their survival (Dickson and Beier, 2007; Laing, 1988; Logan and Irwin, 1985; Riley and Malecki, 2001; Seidensticker et al., 1973).

In Argentina, the effects of topographical and human variables or landscape transformations on carnivores have been poorly

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studied. In the Upper Parana Atlantic Forest of north-eastern Argentina, jaguars (*Panthera onca*) and pumas prefer protected areas with presence of native forests, avoiding modified areas and areas accessible to humans (De Angelo et al., 2011; Paviolo et al., 2009). Altrichter et al. (2006) suggested that in the Argentine Chaco, jaguars are isolated by agriculture and high human densities. In western Patagonia, an assessment of potential risks of livestock exposure to predation showed that puma occurrences were positively associated with proximity to forested habitats and topographic heterogeneity (Kissling et al., 2009). Also in northwest Patagonia, pumas showed no aversion to the use of conifer plantations, contrary to culpeo fox, that was less detected in this type of plantations and showed a preference for native vegetation (Lantschner et al., 2012). Contrasting with these results, in central Chile, culpeo fox was abundant in conifer plantations and scarcely used native vegetation, preferring open habitats and sites close to roads (Acosta-Jamett and Simonetti, 2004).

In North America variation in the density of the wolf (*Canis lupus*) was explained by prey availability and use of areas away from humans (Fuller et al., 2003; Mladenoff et al., 1995). Several studies have suggested that the creation of protected areas is only a palliative measure for the preservation of top carnivores; moreover, if protected areas are small, do not have a healthy native prey assemblage or are surrounded by human populations, they may fail to meet their objectives (Woodroffe and Ginsberg, 1998; Woodroffe et al., 2005). In dry environments low prey density during the drought periods determines a corresponding low density of predators (Holmgren et al., 2006) which highlights the need for larger protected areas in this type of environment and the need to monitor their effectiveness.

Because the occurrence of top carnivores is influenced by positive or negative relationships between complex environmental factors and human activities (Fuller et al., 2003; Hirzel et al., 2002; Naves et al., 2003; Riley and Malecki, 2001; Seidensticker et al., 1973), further case studies are needed to better understand distributions of top carnivores and be able to design general management actions. In the present study, we evaluated the impact of land use changes and topography on terrestrial top carnivores in central Argentina. Top predators of the high mountains of central Argentina include the puma and an endemic culpeo fox (*Pseudalopex culpaeus smithersi*). The puma occurs in most of the American continent and is the largest cat in central Argentina. The puma persists in much of its historical range; however, it has disappeared from areas with intensive human development (Currier, 1983). The culpeo fox is restricted to South America and is the second largest canine within its range, and the largest within the genus. It is distributed from northern Ecuador to southern Chile and Argentina, along the foothills of the Andes, including Tierra del Fuego, and throughout the Argentine Patagonian steppe. It is represented by six subspecies, two of which have isolated populations, such as the target species *P. c. smithersi*, a subspecies endemic to mountains of central Argentina (Novaro, 1997). Both carnivores prey on domestic livestock and are therefore in conflict with humans (Pia, 2004); hence, knowledge on the occurrence of puma and culpeo fox might help to mitigate conflicts with humans and to collect baseline information for devising conservation strategies for these species.

Our study area included a national park and a similar area adjacent to the park in the high mountains of Córdoba, the only region in central Argentina where pumas and culpeo foxes are known to be sympatric. These carnivores feed on the same small prey (mainly rodents) and present a high trophic overlap and low dietary breadth, possibly because of the lack of large native herbivores since the last century as a consequence of human-induced landscape modifications and hunting (Pia, 2011; Pia et al., 2003). Since the protected area was created in 1996, hunting was prohibited and livestock completely or partially removed depending on the area. These actions, which allowed the recovery of the vegetation and consequently an increase in abundance of small mammals (Pia et al., 2003), are expected to promote an increase of pumas and culpeo foxes within the national park. However, landholders claim that livestock predation by both top carnivores is equal to or higher outside than inside the park.

We hypothesized that puma and culpeo occurrence is influenced by prey abundance, hunting pressure and refuge availability. Accordingly, our objectives were to determine if the occurrence of these carnivores varied under different management and degradation conditions and to assess the effect of local environmental and human variables. We predicted that both carnivores will be more frequent within the park due to the recovery of native vegetation and consequent high abundance of rodents, their main prey (Pia, 2011; Pia et al., 2003), reduced hunting pressure and greater refuge availability than in the area surrounding the protected area. In addition, we predicted that outside the park, puma and culpeo fox will be more frequent at greater distance from human settlements and at sites with a high proportion of rock outcrops, which could be used as hiding and breeding areas.

2. Materials and methods

2.1. Study area

The study area was located in the high Córdoba Mountain range (Córdoba province, central Argentina, 31° 34′ S, 64° 50′ W). The mountain range has a north–south direction and a maximum elevation of 2884 m asl. Mean temperature at 2100 m asl for the coldest and warmest months was 5.0 and 11.4 °C, respectively, with no frost-free month (Cabido and Acosta, 1985). Mean annual precipitation was 920 mm, with 83% of the rainfall concentrated in the warm months, determining a long dry season which lasts from May to September or November depending on the year (Colladon, 2002). The landscape is dominated by granite outcrops (22% of the surface area), intermingled with a mosaic of tussock grasslands, short forbs and grasses, high altitude forests or shrublands dominated by *Polylepis australis*, and areas with exposed rock surfaces due to soil erosion. The main economic activity in the area is livestock husbandry (cattle, sheep, horses and goat), which began in the 17th century. Livestock is the main driver affecting vegetation composition at the local scale (Cingolani et al., 2008; Renison et al., 2010).

Quebrada del Condorito National Park (hereafter "the park") was created in 1996 and covers an area of 26,000 ha (Fig. 1). Within the park poaching has been greatly reduced since its creation. Livestock inside the park began to be removed in 1998 and during our study, livestock density was null or very low (0–0.4 Livestock units per hectare). Livestock reduction resulted in an increase in vegetation cover and height, which in turn contributed to an increased presence of rodents (Pia et al., 2003). The lands surrounding the park were declared Provincial Water Reserves (117,000 ha); however, they continue to be privately owned and traditional livestock management is still practised at relatively high densities (1.1–4.8 livestock units per hectare), which keeps vegetation short (Cingolani et al., 2004, 2008) and reduces small mammal abundance (Pia et al., 2003).

2.2. Occurrence data

Due to the secretive behaviour and low densities of top carnivores, occurrence was measured by counting the number of signs, which included tracks, feces, or direct sightings of culpeo foxes and

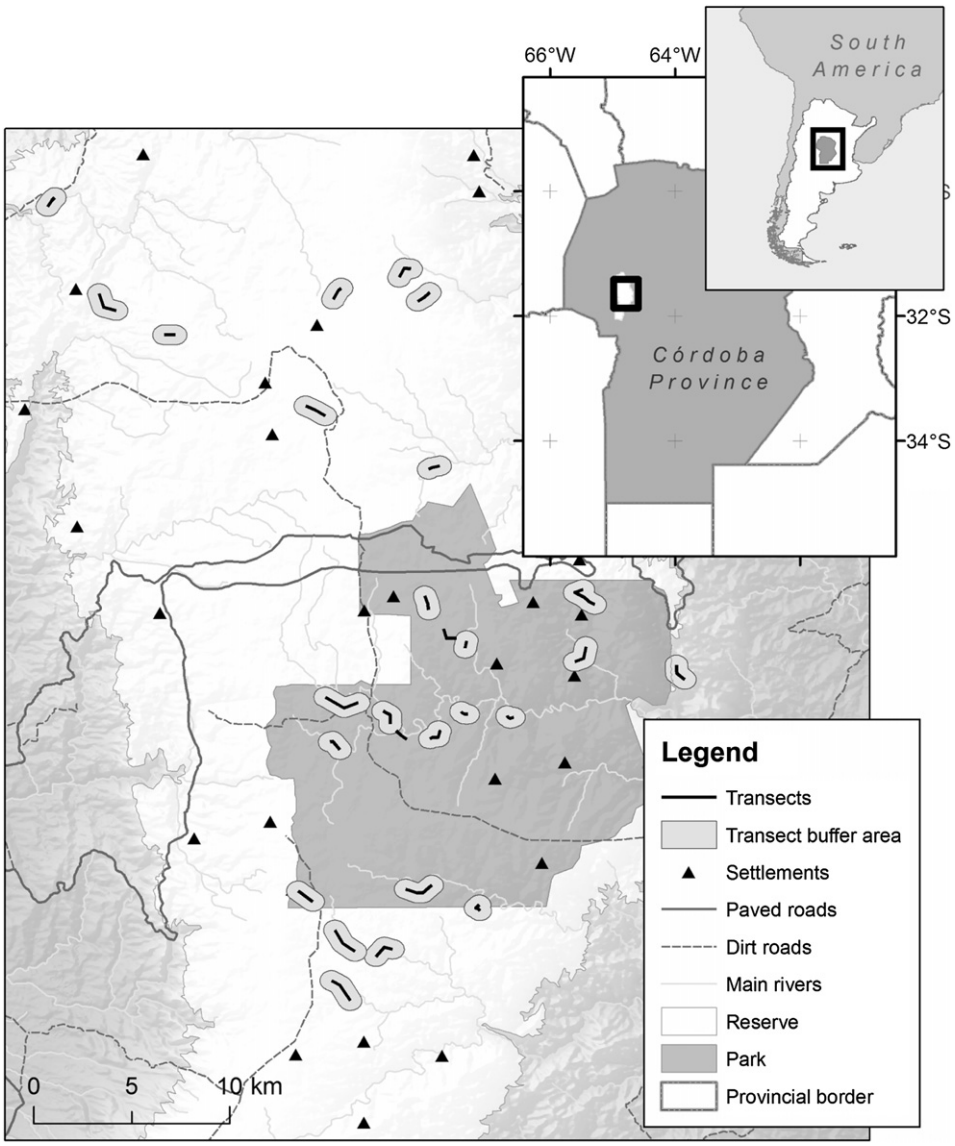

Fig. 1. Map of the study site with locations of transects, buffer areas, human settlements and protected areas in the mountains of central Argentina.

pumas. To count signs, 14 transects were established inside the park and 13 outside the park (5 m × 1000 m, Fig. 1). Transects were set up on natural sandbanks accumulated along riversides and surveys were conducted by walking slowly along transects; signs were recorded and assigned to either of the species. Unidentifiable tracks were excluded from the analyses. We selected sandbanks along rivers because within our study area it is the most widespread type of site where footprints can be registered and we considered that there was no reason to suspect that there might be more avoidance of this type of habitat in one area than another (i.e. human visitation was similarly low throughout). Attempts were made to select a wide range of distances to human settlements and proportion of rock outcrop cover, as determined using a geographic information system (GIS) of the area (Cingolani et al., 2004). Transects were sampled twice between 2007 and 2008. Number and area of transects were determined from a preliminary study and according to availability of sandbanks that permitted the identification of signs (Beier and Cunningham, 1996; Pia, 2008; Smallwood and Fitzhugh, 1995; Stander, 1998). Transects were located as far from each other as possible to better achieve independence among them (see Fig. 1). Minimum distance between each transect was 1500 m. Such distance was defined considering the study area and the small number of adequate sampling sites, with no alternative scenarios available (i.e., no other Park within the eco-region).

2.3. Explanatory variables

The variables quantified were: (1) location relative to the protected area (categorical: inside and outside the park), (2) distance from human settlements (continuous) and (3) proportion of rock outcrops (continuous) surrounding each transect. These variables were selected because they are considered of great importance for the study species (Pia et al., 2003) and in previous studies have explained the occurrence of other important organisms in the area (Cingolani et al., 2008; Renison et al., 2006, 2010). The areas inside and outside the park differed in several aspects, mainly hunting pressure, livestock density, vegetation type and height, and presence of rodents as small prey. The distance from human settlements and proportion of rock outcrop were measured on human settlement and vegetation GIS layers based on a pixel width of 30 × 30 m (Cingolani et al., 2004, 2008). Distance to settlements was measured as the distance from the closest human settlement

to the centre of transect. Settlements were represented by a single house or farm as no towns exist in the study site. For the proportion of rock outcrops, a buffer area of 500 m from any transect point was delineated (Dickson et al., 2005) and the number of pixels corresponding to the outcrops was counted to calculate the percentage (Fig. 1). From previous studies we know that the percentage of rock outcrops remains fairly correlated when considering buffer zones of different sizes. We considered using other variables such as distance from roads and proportion of each vegetation type but given we only had 27 data points (transects) we preferred to maintain a low number of explanatory variables which we selected using expert knowledge as suggested by Flom (2007).

2.4. Statistical analysis

Since the number of signs is a variable based on counts, generalized linear models (GLM) with Poisson distribution and log-linked function were used for analysis (Guisan and Zimmermann, 2000; McCullagh and Nelder, 1989). The two carnivore species were analysed separately using as response variables the sum of the number of signs registered in each transect during the two study years, one categorical and two continuous explanatory variables. Residuals were tested for normality and homoscedasticity.

3. Results

Puma signs were 33 times and culpeo signs 19 times more abundant inside than outside the park (Fig. 2a and b), and accordingly inside the park we recorded a high proportion of transects with presence of signs while outside the park we recorded few transects with sign presence. Overall, puma signs were about 3.5 times less frequent than culpeo signs (mean signs: 105 and 356 for puma and culpeo, respectively).

Distance from settlements had a different effect on the relative abundance of signs of both carnivore species. A higher occurrence of puma signs was recorded at sites away from settlements inside the park; however, outside the park, puma signs were almost null throughout the range of distances evaluated (distance from settlement $\chi^2 = 52.5$; $P = 0.05$; distance × location relative to the protected area $\chi^2 = 3.61$; $P = 0.06$, Fig. 2c, Table 1). Culpeo signs increased with increasing distance from settlements outside the park; inside the park, culpeo signs were abundant throughout the studied range of distances (distance from settlement $\chi^2 = 351.8$; $P < 0.001$, distance × conservation status $\chi^2 = 307.1$; $P < 0.001$, Table 2, Fig. 2d).

Proportion of rock outcrops also affected the relative abundance of signs of both carnivore species differently. Occurrence of puma signs increased at sites with high proportion of rock outcrops in the

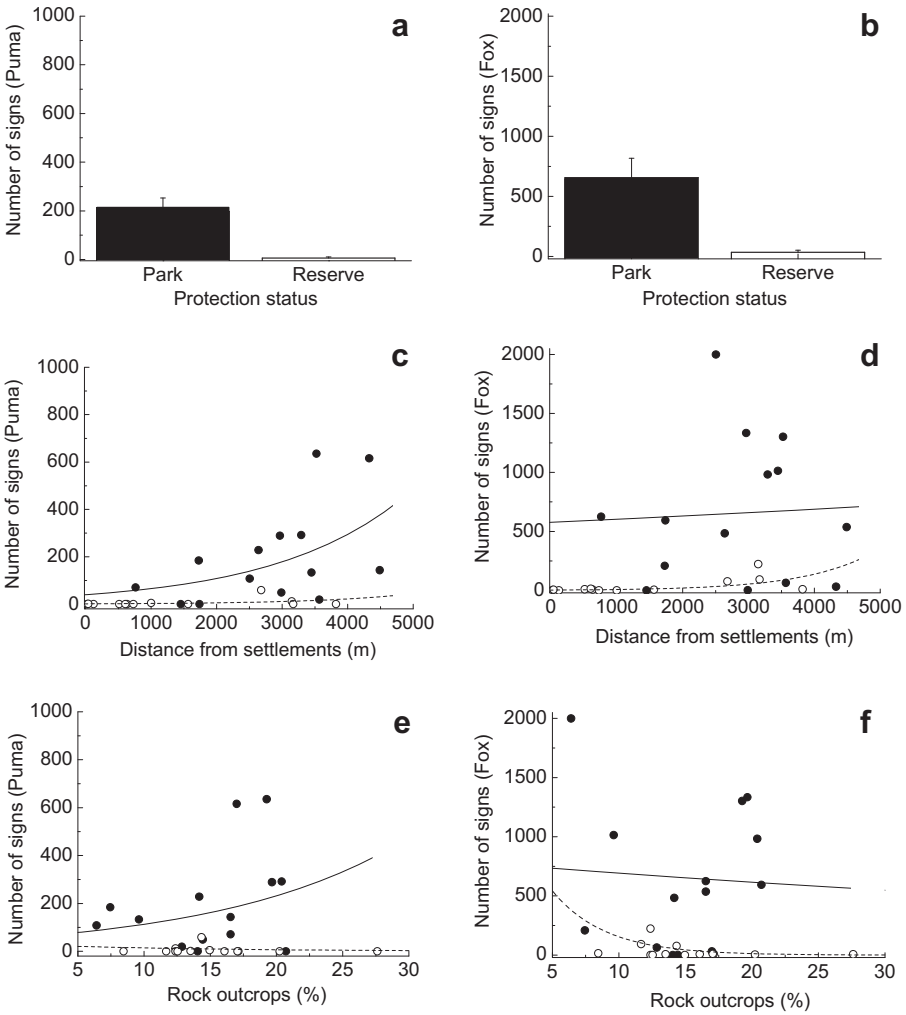

Fig. 2. Effect of protection status (inside and outside the park, a, b), distance to human settlements (c, d) and proportion of rock outcrops (e, f) on the occurrence of puma and culpeo. The black bar and circles correspond to transects within the Park and the white bar and circles, outside the Park. The trend lines indicate the best linear fit to the natural logarithm of the number of signs, cut and solid lines correspond to transects inside and outside the Park, respectively.

Table 1
Output of the generalized linear model with Poisson distribution and log-linked function used to explain the number of puma signs registered in each of the 27 transects distributed in the Cordoba Mountains. We report parameters of model (B), P-values (P), pdds ratio (exp(B)) and standard error.

Parameter	B	P	exp(B)	Standard error
Intercept	1.5056	0.007	4.507	0.557
Park	1.1017	0.052	3.009	0.567
Distance from settlement	0.0007	<0.001	1.001	0.943
Rock outcrops	−0.0757	0.035	0.927	0.036
Park * Distance from settlements	−0.0002	0.057	1.000	0.965
Park * Rock outcrops	0.1476	<0.001	1.159	0.036

park area but not outside the park, where puma signs were almost absent (proportion of rock outcrops $\chi^2 = 4.4$; $P < 0.05$; rock outcrops × location relative to the protected area $\chi^2 = 16.5$; $P < 0.001$, Table 1, Fig. 2e). Culpeo signs decreased only very slightly at sites with a high proportion of rock outcrops inside the park and decreased sharply in areas with similar characteristics outside the park (proportion of rock outcrops $\chi^2 = 132.8$; $P < 0.05$; rock outcrops × location relative to the protected area $\chi^2 = 119.3$; $P < 0.05$; Table 2, Fig. 2f).

4. Discussion

Our results clearly demonstrate the importance of conservation status on the occurrence of top carnivores in the high Córdoba Mountains, where the existence of a 12-year-old protected area presumably boosted puma and culpeo abundance, as judged by an impressive 33 and 19-fold higher number of puma and culpeo signs recorded within than outside the park. Distance from human settlements also explained top carnivore abundance in the study area, whereas availability of refuge sites, as indicated by the proportion of rock outcrops, was positively related to puma abundance. By contrast, culpeos appeared to prefer areas away from rock outcrops.

We hypothesized that the occurrence of pumas and culpeo foxes would be determined by prey availability, hunting pressure and refuge availability. Firstly, prey and refuge availability are greater inside the park area, where the low density or absence of livestock has produced an important increase in plant biomass (Cingolani et al., 2004; Pia et al., 2003). Vegetation recovery provides increased year round food and refuge availability for prey. Given the long dry season in our study area, increased food availability during the dry season should therefore increase in carnivore occurrence. Secondly, tall vegetation offers effective refuge from humans and could increase carnivore occurrence, especially of culpeos, which may easily hide in medium-height vegetation.

Mortality of long-lived species with low reproduction rates, such as most large carnivores, is mainly caused by humans (Naves et al., 2003; Woodroffe and Ginsberg, 1998). In particular and in our study area the puma is persecuted to reduce livestock predation. This threat was recorded in a survey to farmers living in areas surrounding the park (Pia, 2004), and in several studies that found negative associations between human presence and occurrence of carnivores (pumas: Riley and Malecki, 2001; wolves: Jędrzejewski et al., 2004; felids of South America: Acosta-Jamett and Simonetti, 2004; De Angelo et al., 2011; Lantschner et al., 2012). Differences in the occurrence of carnivores inside and outside the park may be due to difficulties in establishing their territory outside the park because of intense human activity; therefore, top carnivores may be failing to disperse from their maternal territory (Dickson and Beier, 2007; Woodroffe and Ginsberg, 1998). Pumas and culpeos are hunted outside the park, where livestock husbandry is intense and the local extinction of large native prey and reduced availability of small prey increase the risk of livestock predation by top carnivores (Pia et al., 2003). For example, farmers living far from the park reported higher losses of livestock than did farmers living near the park, probably because carnivores have access to the park to feed on abundant native prey (Pia, 2004). Consequently, the risk of mortality for top carnivores is much higher outside the park where both species are persecuted.

In our study, the presence of settlements and roads was associated with human activities which presumably include poaching. We assume culpeos to be more easily adapted to human presence than pumas because culpeo signs were equally abundant near and far from settlements inside the park, where hunting is better controlled, but not outside the park where hunting goes largely unchecked and culpeos were abundant only far from settlements, while pumas still persisted in maintaining distance from settlements within the park. These findings are in agreement with other studies reporting that large carnivores used roads more intensively inside protected areas where the species are less persecuted and often more abundant than outside (De Angelo et al., 2011; Dickson et al., 2005; Noss et al., 1996), and that they preferred dirt roads over paved roads (Dickson and Beier, 2007). Moreover, a more generalist and quickly adaptive behaviour of culpeos than of pumas was reported under other circumstances, where for example in central Chile, despite the intense human presence, culpeo fox is commonly found in exotic plantations due to the abundance of roads which allow them to move through different habitats and hunt small mammals (Acosta-Jamett and Simonetti, 2004). On the other hand, overgrazing by livestock causes a decline in small rodent populations, the main prey of the studied carnivores, as well as changes in carnivore diets (Pia, 2011; Pia et al., 2003), which could be another reason why these carnivores are less likely to occur outside than within the park. Thus, human disturbances on herbivore populations and the negative attitude of farmers towards carnivores due to livestock predation (Pia, 2004) may be variables which together determine the occurrence of culpeos and pumas across the study area.

Rock outcrops had a differential effect on both carnivores. They might be an important resource for pumas both to hide from humans or any other threat and to protect their cubs. Accordingly, terrain roughness and vegetation cover explained a major part of the variation in abundance of pumas in North America (Dickson and Beier, 2007; Riley and Malecki, 2001). Inside the park, culpeos appeared to use flatter areas with greater vegetation cover than those used by pumas, perhaps due to their smaller size, the high availability of their main prey, and to avoid the encounter with pumas. In southwester Patagonia detection of culpeo fox was higher in areas with continuous native vegetation due to the great availability of refuge and prey (Lantschner et al., 2012), whereas in central Chile culpeo foxes were more commonly found in open

Table 2
Output of the generalized linear model with Poisson distribution and log-linked function used to explain the number of culpeo fox signs registered in each of the 27 transects distributed in the Cordoba Mountains. We report parameters of model (B), P-values (P), pdds ratio (exp(B)) and standard error.

Parameter	B	P	exp(B)	Standard error
Intercept	4.9047	<0.001	134.919	0.270
Park	1.6291	<0.001	5.099	0.274
Distance from settlement	0.0009	<0.001	1.001	0.00005
Rock outcrops	−0.2498	<0.001	0.779	0.021
Park * Distance from settlements	−0.0009	<0.001	0.999	0.00005
Park * Rock outcrops	0.2382	<0.001	1.269	0.021

areas where main prey are more abundant (Acosta-Jamett and Simonetti, 2004).

We conclude that the creation of the National Park represents a great contribution to the conservation of puma and culpeo fox in the high mountains of central Argentina. Worldwide it is recognized that the long-term persistence of many species, particularly carnivores, depends on protected and buffer areas, which influence species abundance, like in the Atlantic forest of Argentina where the abundance and behaviour of pumas varied among areas with different levels of protection, being the abundance higher in the better protected areas (Paviolo et al., 2009). Thus, the park plays the role of refuge for both carnivores, where habitat quality (refuge availability and low human impact) is suitable for survival, and carnivores benefit in terms of conservation, and less access to livestock, helping to reduce the human conflict. Further researches on both carnivores are needed and given that the greatest long-term threat to carnivores is land conversion (Ginsberg, 2001), the creation of protected areas with connectivity in the region should be considered.

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