Journal for Nature Conservation 56 (2020) 125846

Contents lists available at ScienceDirect

Journal for Nature Conservation

journal homepage: www.elsevier.com/locate/jnc

A small protected area facilitates persistence of a large carnivore in a ranching landscape

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A R T I C L E I N F O

Keywords:
Edge effect
Human-carnivore conflict
Monte desert
Population dynamics
Puma concolor
Retaliatory killing

A B S T R A C T

Assessments of the role that small (< 500 km^2) protected areas play in conservation of large carnivores in landscapes where the species are persecuted are scarce. Using camera-trap sampling we estimated puma (*Puma concolor*) population abundance, site use intensity, and relative abundance of prey in Lihué Calel National Park (320 km^2) and two neighboring livestock ranches in central Argentina. We concurrently assessed rancher attitudes towards puma in relation to livestock predation by this carnivore and retaliation by ranchers in the ranching landscape surrounding the protected area. At least 3–8 adult pumas were recorded within the park while no individuals were detected on private ranchland. Site abundance within the park was positively related to the distance from the park boundary. The overall prey base inside and outside the park was similar. Sixteen out of 17 ranchers reported livestock losses due to puma predation and 76% of ranchers employed lethal control of carnivores to avoid livestock losses, resulting in 16 pumas killed during 2007–2009 in the surveyed ranches. The avoidance by pumas of the park´s border, the absence of puma detections on ranches, the similar prey availability inside and outside the park, and the positive association between rancher's negative perceptions and persecution of pumas suggests that puma occurrence is depressed in ranchlands as a result of human-induced mortality. Our results demonstrate how small protected areas can play a role in maintaining large carnivores within productive landscapes despite harsh persecution. We emphasize the positive role of ranches that do not persecute pumas and the need to facilitate the coexistence between puma and people for the long term conservation of this felid in ranching landscapes.

1. Introduction

Extensive habitat conversion for agriculture and livestock production has resulted in habitat loss and degradation for many large carnivores (Terborgh, 1999). In these modified landscapes, prey depletion (Wolf & Ripple, 2016) and direct human-caused mortality (Treves & Karanth, 2003) frequently occur, resulting in the extirpation of large carnivores (Ceballos, Ehrlich, Soberón, Salazar, & Fay, 2005; Schipper et al., 2008). Consequently, these predators often persist only in extensive protected or remote areas with limited access by humans (Chase-Grey, Kent, & Hill, 2013; Seidensticker, Christie, & Jackson, 1999; Stoner, Wolfe, Rieth et al., 2013).

Large protected areas are needed to conserve large carnivores, but even areas of more than 1000 km^2 could sometimes not be large enough to support viable populations of these species (e.g., Shaffer & Samson, 1985; Schonewald-Cox, Baker, & Bayless, 1988; Woodroffe & Ginsberg, 1998). On the other hand, small reserves (i.e., < 500 km^2) often harbor small populations or subpopulations of large carnivores (i.e., < 25

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https://doi.org/10.1016/j.jnc.2020.125846
Received 5 March 2020; Received in revised form 3 April 2020; Accepted 15 May 2020

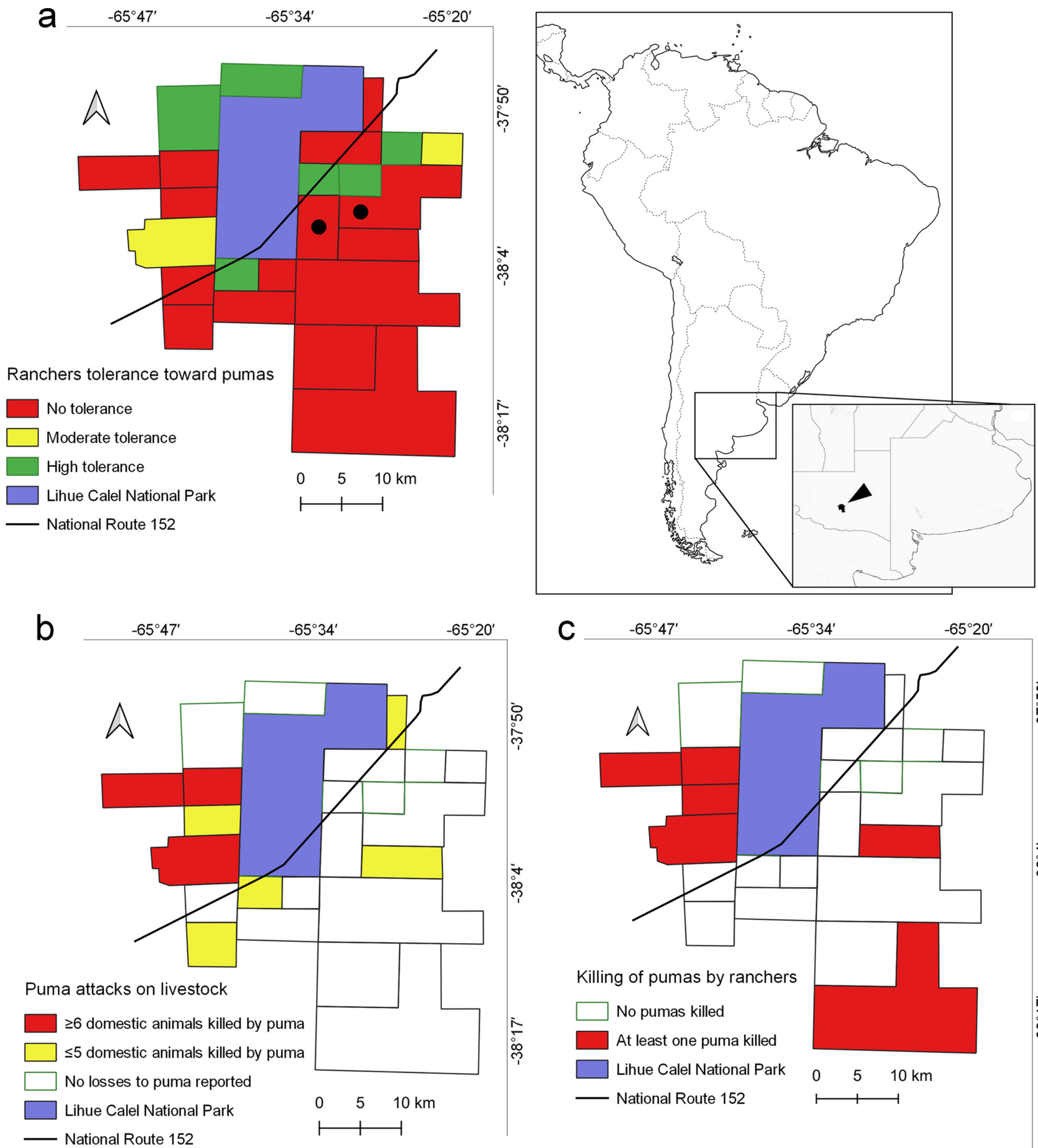

Fig. 1. Study area showing (a) ranchers' tolerance toward pumas, (b) occurrence of puma attacks on livestock, and (c) killing of pumas by ranchers around Lihué Calel National Park during 2007–2009 in the Monte Desert of Central Argentina. Black dots in Fig. 1a indicate the two livestock ranches where camera-trap sampling was performed.

individuals) and have high perimeter/area ratios, resulting in a strong "edge effect" (Woodroffe & Ginsberg, 1998). As a result, the demographic effects of accidental deaths or deliberate killing of carnivores that range beyond reserve borders can extend deep into small protected areas (Balme, Slotow, & Hunter, 2010; Kiffner, Meyer, Mühlenberg, & Waltert, 2007; Loveridge, Searle, Murindagomo, & Macdonald, 2007), compromising their conservation efficacy (Brugière, Chardonnet, & Scholte, 2015; Revilla, Palomares, & Delibes, 2001).

Conserving populations of large carnivores may thus require the management of large landscapes that include both protected areas and surrounding areas under intensive human use. In these diverse landscapes, subpopulations living in protected areas can serve as sources from which dispersing individuals increase the probability of persistence of the population at the landscape level (Hanski & Simberloff, 1997; Noss, Quigley, Hornocker, Merrill, & Paquet, 1996). Small but strictly protected areas can be important in this context as part of a network of interconnected reserves (e.g., Laidlaw, 2000; Carroll, Noss, Paquet, & Schumaker, 2004) or as stepping-stones, that increase the connectivity between relatively isolated subpopulations of large carnivores (Carroll & Miquelle, 2006; Luja, Navarro, Torres-Covarrubias, Cortés-Hernández, & Vallarta-Chan, 2017; Rabinowitz & Zeller, 2010).

Pumas (*Puma concolor*) are large felids (35–85 kg) widely distributed in the Americas, being present from deserts to tropical humid forests and from sea level to 5800 masl (Nowell & Jackson, 1996). Anthropogenic mortality can greatly influence the demography of puma populations, and the spatial heterogeneity of stressors (e.g., hunting pressure) can induce source-sink dynamics at the landscape scale (e.g., Robinson, Wielgus, Cooley, & Cooley, 2008; Cooley, Wielgus, Koehler, Robinson, & Maletzke, 2009; Stoner, Wolfe, Rieth et al., 2013, 2013b; Zanón-Martínez et al., 2016; Paviolo et al., 2018). This indicates that puma populations can be resilient to local anthropogenic mortality and underline the role of immigration and emigration in maintaining the species at the landscape level (e.g., Robinson et al., 2008; Cooley, Wielgus, Koehler, Robinson et al., 2009; Stoner, Wolfe, Mecham et al., 2013; Paviolo et al., 2018). In this context, refugia (e.g., protected areas) of adequate size and protection status (e.g., Andreasen, Stewart, Longland, Beckmann, & Forister, 2012; Stoner, Wolfe, Rieth et al., 2013; Zanón-Martínez et al., 2016) or even areas subjected to light hunting pressure (Cooley, Wielgus, Koehler, & Maletzke, 2009) can act as sources of pumas that repopulate adjacent areas of high hunting pressure.

Conflict with humans is responsible for frequent puma mortality in productive landscapes of South America (e.g., Michalski, Boulhosa, Faria, & Peres, 2006; Guerisoli et al., 2017). In Patagonia and the Monte desert of Argentina, pumas are systematically killed because of the perceived or real threat they pose to livestock, with their hunting encouraged through a state bounty system by some provincial governments (Llanos, Travaini, Montanelli, & Crespo, 2014; Walker & Novaro, 2010). The situation reflects the generally low tolerance of ranchers to share lands with pumas, as is typical with most large carnivores (Treves & Karanth, 2003). However, in a particular landscape, ranchers may show different tolerance levels depending on factors such as perceived risk of livestock predation, historical events, emotional dispositions, cultural and religious practices, or even willingness to collaborate with conservation (Amit & Jacobson, 2017; Dickman, 2010). Thus, assessing local attitudes toward pumas in multi-use landscapes is important to evaluate conflict levels and patterns, since different tolerance levels may drive spatial differences in hunting pressure throughout the productive matrix.

Despite the important and common interplay between protected areas and surrounding human-use matrixes, assessments of the role that small protected areas play in conservation of large carnivores in landscapes where these species are persecuted are scarce (e.g., Ranganathan, Chan, Karanth, & Smith, 2008; Balme et al., 2010; Zanón-Martínez et al., 2016). We studied puma population abundance, intensity of site use, and relative abundance of prey in a small protected area (i.e., 320 km^2) and two neighboring livestock ranches in an agricultural landscape dominated by livestock ranching in semiarid scrublands of central Argentina. We also assessed the spatial heterogeneity of the matrix surrounding the protected area by surveying (1) the attitudes of ranchers towards the puma, and (2) the numbers of livestock depredated by puma and of pumas killed by ranchers. Our ultimate goal was to assess the conservation significance of small protected areas and low-conflict ranches for pumas in the typical livestock-production landscape of the Monte ecoregion, where protected areas are mostly small (i.e., < 500 km^2) and are spatially isolated.

2. Materials and methods

2.1. Study area

The study was conducted in Lihué Calel National Park (ca. 320 km^2; 38°00´S 65°35´W, hereafter 'park') and adjacent livestock ranches (hereafter 'ranches'; Fig. 1) located in the Monte ecoregion of central Argentina (Burkart, Barbaro, Sanchez, & Gómez, 1999). The area has mean daily temperatures that range from 7.8°C in winter to 25.4°C in summer and low, unpredictable annual rainfall (498 ± 141 mm SD). Vegetation is characterized by creosote bush *Larrea* sp. scrublands, small xeric forests and patches of mixed scrubland. An isolated set of bare rock hills (590 masl) is located in the center of the park and provides good cover for pumas (Branch, Pessino, & Villarreal, 1996).

The park is surrounded by ranches (ranging from 22 to 250 km^2) where vegetation structure has been altered due to livestock management (Pereira, Walker, & Novaro, 2012). Landscape physiognomy and management practices in most of these ranches are relatively homogeneous in the region (i.e., current livestock densities ranging between 9 and 21 animals per km^2, paddock rotation, vegetation management with fire, sanitary protocols for livestock; Pereira, 2009). Hunting of wildlife by ranchers is common, and the most targeted species are the introduced wild boar (*Sus scrofa*) and European hare (*Lepus europaeus*), and the native guanaco (*Lama guanicoe*) and armadillo (*Zaedyus pichiy*). These are also the most common prey for pumas in this area (Branch et al., 1996; Pessino, Sarasola, Wander, & Besoky, 2001; Pereira, unpublished). Conversely, livestock is absent within the park, the habitat is relatively undisturbed, and hunting is not permitted there.

2.2. Camera trapping and estimation of puma abundance

Systematic camera trap surveys (Karanth & Nichols, 1998) were conducted in Lihué Calel National Park and two adjacent livestock ranches (55 and 100 km^2; Fig. 1). Camera trap records from these surveys were used to estimate population parameters for pumas, even though the spatial arrangement of camera-traps was dependent upon the original focus of our study, which was to estimate density of Geoffroy´s cats (*Leopardus geoffroyi*) and other small felids (Pereira et al., 2011). Thus, spacing among camera traps was relatively close compared to the large movements of pumas.

Two surveys were performed using the same general methodology. The first survey was carried out only in the park from January to April 2006 and the second was carried out simultaneously in the park and in neighboring ranches from November 2007 to February 2008. Sampling stations were set on trails and dirt roads that were most likely to be frequented by pumas (Kelly et al., 2008; Paviolo, di Blanco, De Angelo, & Di Bitetti, 2009). Each sampling station consisted of a pair of camera traps facing each other and programmed to obtain pictures on a 24 h basis. No bait was used to attract animals to the traps.

Camera stations were spaced at a minimum distance of 0.57 km and a maximum distance of 4 km (mean distance = 1.27 km) ensuring that any puma present in the study areas had a probability greater than zero to be captured by at least one of the sampling stations. However, mean distance among cameras was lower within the park (up to 1.19 km) to accommodate an adequate number of trap stations in a small area. The first and second surveys lasted 74 and 94 days, respectively.

Camera traps were set up in half of the sampling stations for the first half of the surveys, after which the stations were moved to the remaining sampling stations for the rest of the survey, following the protocol described in Pereira et al. (2011). Thus, each sample was treated as coming from a 37-day-long survey in 2006 with 27 sampling stations, and a 47-day-long survey in 2007–2008 with 40 sampling stations (21 within the park and 19 in the ranches). Overall sampling efforts were 1002 trap-days at the park in 2006, 987 trap-days at the park in 2007–2008 and 893 trap-days at the ranches in 2007–2008.

Pumas photographed were identified following Kelly et al. (2008) and Negrões et al. (2010); three of the authors independently classified individuals, noting the distinguishing characteristics of each animal (e.g., scars, ear nicks, tail-tip coloration, undercoat spot patterns, coloration on the underside of legs, tail carriage, etc.). Pictures that failed to present diagnostic details to identify individuals were discarded from this analysis (n = 4). Record or "capture" histories for individual pumas were developed based on each investigator's identifications, and an independent estimation of the abundance of pumas was obtained using the classification of each author. When an individual was captured more than once in a sampling station within a period of 2 h, only the first photograph of that animal was considered as a record.

Population abundance of pumas was estimated using capture – recapture (CR) models in program CAPTURE (Rexstad & Burnham, 1991). To meet the assumption of population closure (i.e., no births, deaths, or emigration/immigration occur during the sampling period), surveys lasted up to 94 days, in agreement with Kelly et al. (2008) and Paviolo et al. (2009). To reach an individual probability of capture of > 0.1 per trapping occasion (Otis, Burhnam, White, & Anderson, 1978; White, Anderson, Burnham, & Otis, 1982), two successive days were pooled as one trapping occasion (e.g. days 1–2 = first trapping occasion). Thus, the trapping history of each individual consisted of a string of 19 trapping occasions in 2006 and of 24 trapping occasions in 2007–2008. CAPTURE provides population estimates using different models (for details, see White et al., 1982); since model Mh (which assumes heterogeneity among individuals in their capture probabilities) was the one that best fitted (i.e., first in rank) all CR histories, results of model Mh (Jackknife estimator) are reported.

The low number of puma captures at different camera-trapping stations precluded us to estimate population density by employing spatial capture-recapture (SCR) models (Royle, Nichols, Karanth, & Gopalaswamy, 2009). As density estimates from non-spatial CR using ad hoc approaches to estimate sampling area (i.e. mean maximum distance moved; MMDM) can produce biased results (Tobler & Powell, 2013) we did not attempt to estimate densities but rather present abundance estimates (i.e., population size). The minimum convex polygon encompassing all camera trapping stations was 31.1 km^2 in the park in 2006, 32.2 km^2 in the park in 2007–2008, and 49.6 km^2 in the ranches in 2007–2008.

2.3. Intensity of site use

Given that pumas were not detected outside the park (see Results) we analyzed the effect of the park border on area used by puma within the park with a site-abundance model (Royle, 2004) within a Bayesian modeling framework. As detections of pumas among sites were not spatially independent, we interpreted estimates of site abundance as intensity of site use (i.e., the number of times individuals were using the sites) rather than strictly the number of individuals at a site. We pooled the 2007–2008 data (only for camera trap stations located within the park) into sampling occasions of 5 sampling nights, with detections of individuals considered temporally independent if they were separated by at least 2 h.

The modeling was undertaken in R 3.4.1 (R Development Core Team, 2010) using the R2WinBUGS package (Sturtz, Ligges, & Gelman, 2005) to call WinBUGS (Lunn, Thomas, Best, & Spiegelhalter, 2000) to conduct the Gibbs sampling for which we ran three chains of 35,000 iterations, discarding the first 10,000, and thinning by 15 iterations. Convergence was confirmed by scale reduction factors of < 1.01 and visual inspection of trace plots (Gelman & Hill, 2007). To estimate the relationship between mean site abundance and distance from the park boundary we randomly sampled 100,000 values with replacement from the posterior distributions of the parameter estimates for abundance.

2.4. Prey availability in the park and ranches

The capture frequency of prey species (i.e., number of independent photographs of each species per 100 camera-trap days) was estimated and used as an index of prey relative abundance at both the park and ranches, based on photographs taken during the 2007–2008 survey. Additionally, the proportion of camera-trapping stations with positive records of each prey species was considered as a measure of prey distribution at both sites. Prey species considered were wild boar, European hare, Patagonian mara (*Dolichotis patagonum*), guanaco, and armadillo (following Branch et al., 1996; Pessino et al., 2001; Pereira, unpublished). Photographs of the same species recorded from the same camera-trap station > 1 h apart were considered as independent records. The use of indices to compare relative abundances has been criticized since these measures do not account for imperfect and variable detection (e.g., Jennelle, Runge, & Mackenzie, 2002; O'Brien, 2011; Sollmann, Mohamed, Samejima, & Wilting, 2013). However, relative abundance indices have received some validation in the context of camera trapping studies with several species (e.g., Carbone et al., 2001, 2002; O'Brien, Kinnaird, & Wibisono, 2003; Rovero & Marshall, 2009; Balme et al., 2010; Jenks et al., 2011; Chase-Grey et al., 2013). As the sampling effort in the park and on ranches was nearly equal (987 vs. 893 camera trap days), raw counts of each species (i.e., number of independent photographs) were compared between sites using a Poisson *t*-test, conducting the analysis in R 3.4.1, glm function (R Development Core Team, 2010). The proportion of camera-trapping stations with positive records of each prey species was compared between the park and ranches using a Fisher Exact Test.

2.5. Livestock losses, rancher attitudes toward puma and the influence of the proximity to the protected area

To evaluate attitudes toward pumas in the region, semi-structured interviews were conducted for livestock ranchers on properties adjacent to or near (up to 30 km from) the protected area (n = 17). Interviewees selected in each ranch were those with > 3 years of residence on the ranch and with active participation in livestock management practices. A verbal informed consent was obtained from each interviewee after explaining the nature and full description of the study. Ethical principles such as respect for the participant, no coercion, avoidance of undue intrusion and no use of deception were fully respected through the interview process. Each rancher was also informed that the answers would be anonymous and confidential. Our work complied with all the ethical guidelines and requirements of Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET) of Argentina.

Interviews (one per ranch) were conducted personally, as a friendly talk on each property, and were focused on the following topics: (1) causes and number of losses of domestic animals, especially those resulting from pumas and other predators during the last year; (2) attitudes (i.e., tolerance) toward pumas and puma control-methods employed in the ranch; and (3) number of pumas killed during the last three years (2007–2009). Tolerance of ranchers to the presence of pumas in their lands was classified as "high" (i.e., puma is not hunted even if losses due to predation are recorded), "moderate" (i.e., up to five domestic animals lost due to puma predation per year are tolerated), or "no tolerance" (i.e., puma is constantly persecuted even when no livestock losses occur). The relationship between the proximity to the park and ranchers´ perception towards puma depredation of livestock as well as reported livestock losses to puma depredation were examined using logistic and linear regression, respectively. Proximity to the park was estimated as the linear distance between the center of each ranch to the nearest protected area border; similar results were obtained using the closest linear distance between the park and the ranches borders. When analyzing ranchers' tolerance of puma depredation, ranches with moderate and high tolerance were grouped together due to small sample size. To test for a relationship between ranchers' tolerance toward puma and the number of pumas reported killed, a Poisson *t*-test in a Bayesian modeling framework was used. Modeling was also undertaken using the glm function in R and evaluation of convergence as the site abundance modeling, running 3 chains of 10,000 iterations, discarding the first 1,000 iterations and thinning by 2 iterations.

Whether no tolerance was associated with more pumas killed compared to ranches that reported moderate or high tolerance was tested by randomly selecting 10,000 values from the posterior distributions of the *t*-test with replacement and recording the proportion of times that the expected number of pumas killed was greater in ranches with no tolerance compared to ranches with moderate or high tolerance. No difference between groups is indicated when the probability of a difference between the two groups is 0.5 and increases as values approach 0 or 1.

Finally, both the attitudes of ranchers toward puma and livestock losses due to predation were mapped to evaluate landscape-level spatial patterns (total area of the landscape studied = 1,722 km^2). For mapping purposes, killing of pumas by ranchers were considered as occurred vs. not occurred, whereas the number of domestic animals killed by pumas on each ranch during the study was divided into two categories ($\leq$5 animals killed vs. $\geq$ 6 animals killed) based on the criteria used to define ranchers' tolerance.

3. Results

3.1. Puma identification, population abundance, and turnover

In 2006, 19 independent records of pumas were obtained in the park, representing a capture success of 1.90 records per 100 trap-days. In 2007–2008, 39 independent records were obtained in the park (capture success = 3.95 records per 100 trap-days) and no record was obtained in the ranches. The three investigators independently classified the photos as belonging to 3 to 4 different adult pumas plus 2 to 3 non-independent juveniles in 2006 and 5 to 7 different adults plus 2 to 3 non-independent juveniles in 2007–2008 (Table 1). Estimates of puma abundance using CAPTURE ranged from 3 to 4 adult individuals in 2006 and 6 to 8 in 2007–2008, although confidence intervals significantly increased for the second survey estimates (Table 1). At least two individuals (an adult male and an adult female) were recorded in the park during both the 2006 and the 2007–2008 surveys.

3.2. Intensity of site use in the park

Mean estimated site abundance was 2.3 (95% credibility interval 1.6–3.2), detection was estimated at 0.08 (95% credibility interval 0.02–0.16), and derived occupancy 0.94 (95% credibility interval 0.48–1). The distance from the park boundary had a positive effect on the probability of site use, with 86% of the values from posterior distribution > 0, indicating that the distance from the park boundary is expected to positively affect site use by puma in the large majority of occasions. Mean estimated intensity of site use increased from 1.56 (95% credibility interval 0.48–7.19) at the park boundary to 3.31 (95% credibility interval 0.92–15.81) at 3.5 km away from the park boundary.

3.3. Prey availability in the park and ranches

Overall, 416 independent pictures (189 in the park and 227 in the ranches) from the five prey species considered were obtained (Table 2). There were no significant differences between the frequency that prey, as a whole, were recorded in the park and ranches (Wilcoxon signed rank test $p = 0.79$). European hare was the most frequently photographed species at both sites (Table 2), but the number of records was significantly higher in ranches ($p = 0.01$). Count of Patagonian maras was also significantly higher in ranches ($p < 0.01$), whereas the opposite pattern was found for guanacos ($p < 0.01$). Non-significant differences in counts between sites were found for wild boars ($p = 0.70$) and armadillos ($p = 0.33$). Similarly, a significantly higher proportion of camera-trapping stations with positive records of European hares ($p = 0.01$) and Patagonian maras ($p < 0.01$) were found in ranches than in the park, whereas this proportion for guanacos ($p < 0.01$) was significantly higher in the park than in ranches. No significant differences were found in the proportion of camera-trapping stations with positive records of armadillos ($p = 0.19$) and wild boars ($p = 0.74$) between sites (Table 2).

3.4. Matrix heterogeneity for livestock attacks, attitudes of ranchers, and pumas killed

Sixteen out of 17 livestock ranchers reported losses due to predation by carnivores during the study period, comprising 70 domestic animals lost, including cattle, horses, goats, domestic pigs, and poultry. According to ranchers, predation by pumas accounted for 49% of total kills, which included cattle (n = 23 kills), goats (n = 6), and horses (n = 5). Predation mortalities represented on average 0.1%, 2.0%, and 2.7% of the total number of cattle, goats, and horses, respectively, present in the surveyed ranches each year. Predation by puma was responsible for 19% of livestock mortalities reported, being the third most important cause of livestock mortality after disease and emaciation. There were no significant relationships between distance from the park boundary and the number of domestic animals killed (linear regression, $p = 0.88$) or between distance from the park boundary and tolerance toward pumas (logistic regression, $p = 0.45$).

Seventy-six percent of ranchers employed lethal control of carnivores (e.g., trapping, shooting) to avoid livestock losses, with 100% of interviewees believing that puma populations should be controlled. Sixteen pumas (8 adults, 4 juveniles still dependent on their mothers, and 4 cubs within dens) were reported as being killed by ranchers during 2007–2009 in the surveyed ranches. There was a 96% probability that more pumas were killed on ranches with no tolerance of puma depredation compared to those with moderate or high tolerance, with the mean number of pumas reported killed on ranches with no tolerance (n = 11 ranches) being higher (0.63 pumas per year, 95% credibility interval 0.26–1.17) compared to ranches with moderate (n = 3) or high (n = 3) tolerance (0.17 pumas per year, 95% credibility interval 0.00–0.62).

Mapping the spatial patterns of puma persecution demonstrated a relatively large area (ca. 654.9 km^2; 38% of the studied landscape area) over which puma are not persecuted, which is centered on the national park, encompassing several ranches with high or moderate tolerance (Fig. 1a). Concurrently, however, three large to medium sized ranches where attacks on domestic animals and retaliatory killing of pumas occurred frequently were located to the west, east, and southeast of the park. These three ranches were adjacent to other ranches with low tolerance for pumas (Fig. 1).

Table 1
Numbers of adult pumas (*Puma concolor*) identified by different investigators and estimates of mean number of captures per individual, capture probability, and population size in Lihué Calel National Park, Monte Desert, Argentina.

Survey	No. of adult individuals recorded			Mean no. of captures per individual (range)	Capture probability	Population size	
	Males	Females	Unknown			Abundance estimate	95% CI
2006							
Inv. 1	1	2	0	4.7 (3–8)	0.228	3	3–3
Inv. 2	1	2	1	3.5 (2–5)	0.171	4	4–4
Inv. 3	1	2	0	4.7 (3–7)	0.246	3	3–3
2007-2008							
Inv. 1	2	4	0	4.5 (1–8)	0.148	7	7–14
Inv. 2	3	4	0	4.6 (1–9)	0.156	8	8–33
Inv. 3	2	3	0	5.8 (1–10)	0.181	6	6–13

Table 2
Total number of independent photographs, average number of photographs per camera trapping station, and proportion of camera trapping stations with positive records of prey species of puma (*Puma concolor*) in Lihué Calel National Park (LCNP) and adjacent livestock ranches, Monte desert, Argentina.

Species	LCNP			Livestock ranches		
	No. of independent photographs	No. of photographs per station (Mean ± SD)	Proportion of stations with records	No. of independent photographs	No. of photographs per station (Mean ± SD)	Proportion of stations with records
European hare (*L. europaeus*)	134	6.4 (9.3)	0.57	169	8.9 (8.2)	0.95
Patagonian mara (*D. patagonum*)	10	0.5 (1.9)	0.09	44	2.3 (2.7)	0.79
Guanaco (*L. guanicoe*)	27	1.3 (2.1)	0.48	2	0.1 (0.5)	0.05
Armadillo (*C. villosus* and *Z. pichiy*)	5	0.2 (0.4)	0.24	2	0.1 (0.5)	0.05
Wild boar (*S. scrofa*)	13	0.6 (1.2)	0.33	10	0.5 (0.9)	0.26

4. Discussion

Pumas were only recorded inside the park, with a small number of adult individuals (at least three in 2006 and five in 2007–2008) recorded in the sampled area inside the park (ca. 10% of the park's total area). Reproduction inside the park was evidenced by records of dependent juveniles in both surveying periods. Conversely, no pumas were detected in 893 nights of camera trap sampling in livestock ranches surrounding the park, even though the overall prey base inside and outside the park was similar. This could be the result of a low camera-trapping effort, a lower puma density than in the park, and/or a puma behavioral response that may have reduced their detectability in ranches, such as evading internal roads to avoid encounters with ranchers and their dogs. However, presence and reproduction of this species in ranches were derived from records of several individuals (adults, cubs and juveniles) killed there by ranchers and through the existence of livestock depredation attributed to this felid.

Although variable, we showed greater site use by pumas in the interior of the park. Given the absence of puma camera-trapping records in livestock ranches, and the positive association between rancher's negative perceptions and persecution of pumas during the study period, we hypothesize a negative effect of retaliatory killing on the occurrence of these predators in the park border and adjacent ranchlands (i.e., a relatively strong edge effect; Woodroffe & Ginsberg, 1998). Spatial and demographic characteristics of large carnivores inhabiting in close proximity to the protected area borders can be significantly impacted by anthropogenic pressures, affecting mortality rates, population density, or reproductive performance (Balme et al., 2010; Loveridge, Valeix, Elliot, & Macdonald, 2017). Pumas perceive humans as "super predators" and respond to direct and indirect cues indicative of human presence (Smith et al., 2017), which can contribute to alter puma behavior in protected area borders and may explain limited puma use of Lihué Calel park borders.

The home-range size of pumas can vary from 100 to > 700 km^2 in males and from 30 to 300 km^2 in females (Elbroch & Wittmer, 2012; Grigione et al., 2002; Logan & Sweanor, 2010); while male home ranges can be relatively exclusive, they usually extensively overlap several female home ranges (Logan & Sweanor, 2010). These characteristics of the puma spatial ecology illustrate how small Lihué Calel National Park (320 km^2) is in relation to the spatial requirements of this predator, having space to accommodate just a small number of individuals. Other studies have found a few pumas inhabiting relatively small protected areas (< 350 km^2) within anthropogenic matrixes (Gilad, Janecka, Armstrong, Tewes, & Honeycutt, 2011; Miotto, Rodrigues, Ciocheti, & Galetti, 2007; Zanón-Martínez et al., 2016), with puma populations in these areas likely maintained through immigration of individuals from neighboring occupied habitat patches. Conversely, pumas have been shown to be extirpated from small areas without connectivity to puma sources (Beier, 1993; Chiarello, 1999), which suggests that pumas are sensitive to the loss and fragmentation of habitat when connectivity among relatively small protected areas or habitat remnants is lost or reduced beyond minimum thresholds (Crooks, 2002).

The long-term persistence and, in fact, even the current existence of pumas in this small protected area is unlikely if no source of pumas outside the park is available, allowing pumas to disperse into the park. Pumas exhibit high dispersal abilities (Elbroch, Wittmer, Saucedo, & Corti, 2009; Hawley et al., 2016; Thompson & Jenks, 2010) and thus can potentially reach different habitat patches irrespective of their size and remoteness if the landscape matrix is conducive to movement (but see Tucker et al., 2018). As the prey base for pumas (both native and exotic, including livestock) is not a limiting factor on ranches of the southern Monte (this study; Branch et al., 1996; Rodríguez, 2009; Rodríguez & Barauna, 2015), human-induced mortality is, therefore, likely the main factor affecting puma population dynamics across this landscape.

Puma populations are highly resilient to local anthropogenic mortality, being immigration and emigration key processes in maintaining the species at the landscape level (e.g., Robinson et al., 2008; Cooley, Wielgus, Koehler, Robinson et al., 2009; Stoner, Wolfe, Mecham et al., 2013). In large sheep ranches of southern Patagonia, pumas are systematically killed by ranchers, but their numbers remain high likely due to recolonization from adjacent parks and/or ranches where there is no hunting (Walker & Novaro, 2010). In our study area, pumas persist in the mosaic landscape dominated by livestock ranches typical of the Monte ecoregion, where the spatial heterogeneity observed in puma tolerance and persecution (Fig. 1) could be inducing a source-sink population dynamics (Novaro, Funes, & Walker, 2005; Stoner, Wolfe, Mecham et al., 2013). In this context, the three large or medium ranches with high conflict and puma deaths may function as ecological sinks, "draining" pumas from adjacent areas. On the other hand, if the absence of records of pumas being killed outside these potential sinks reflect that no hunting is occurring there, and that pumas are reproducing in ranches (supported by records of puma cubs killed there), part of the study area outside the park may be also acting as a source of pumas. This scenario highlights the joint role of the protected area and livestock ranches without puma hunting in maintaining the puma population in the study area.

In North America, source populations that serve to maintain or repopulate small puma populations were estimated to occur over areas as large as 2,200 km^2 (Beier, 1993) or 3,000 km^2 (Logan & Sweanor, 1998). Protected areas in the Monte desert of Argentina cover ca. 26,000 km^2, representing less than 5.5% of this ecoregion surface, with only two of 27 protected areas larger than 2,200 km^2 (Administración de Parques Nacionales, Sistema de Información de Biodiversidad - www.sib.gob.ar). Furthermore, at least 15 of these areas are poorly implemented or are not implemented at all (Duval, Benedetti, & Campo, 2017; Pol, Camín, & Astié, 2006). Thus, the potential of this ecoregional protected-area system to act as the only source of pumas is extremely limited and unlikely to prevent the local extinction of pumas. Effective protection of these predators is likely to require a maximization of reserve sizes or a resolution of conflicts with ranchers to mitigate persecution on private lands. To be effective in increasing the conservation potential of small protected areas for pumas in ranching dominated landscapes, management interventions should focus on both reducing livestock depredation and increasing ranchers' tolerance (see Quiroga, Noss, Paviolo, Boaglio, & Di Bitetti, 2016; Guerisoli et al., 2017). Measures that aim only to combat stochastic processes inside isolated reserves will only serve to exacerbate the hostility between ranchers and protected area managers.

Although pumas have been intensively studied in North America, relatively little research has focused upon addressing persecution in ranching dominated landscapes. We recognize two shortcomings of our study: (1) it was not replicated in space and was only partially replicated in time; and (2) our data and study design do not allow us to extrapolate the observed patterns to other species of large carnivores or landscapes. In spite of this, research of predators in previously unstudied environmental or sociological contexts is important to gain insights into how and why carnivores respond along a spectrum of environmental and anthropogenic factors (Boitani & Powell, 2012; Laundré & Hernández, 2010). Consequently, the information generated in within the ecological and human dimensions contexts by this study not only contribute to a better understanding of puma ecology in the understudied Monte desert, but also are a contribution to understanding the general relationship among carnivores and people.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

M. Romero provided help and advice in the study area. J. Gato assisted during an early stage of interviews. C. De Angelo and Y. Di Blanco collaborated during picture identifications and P. Teta assisted with figure development. We appreciate the thoughtful comments of D. Parker and an anonymous reviewer on an earlier version of this paper. This study was funded by The Rufford Foundation, Secretaria de Ambiente y Desarrollo Sustentable de la Nación, Dirección de Recursos Naturales of La Pampa, Amersfoort Zoo, and Le Parc des Felines. Funds to buy the camera traps were provided by Fundación Vida Silvestre Argentina - WWF, Lincoln Park Zoo, Fundación Antorchas, Idea Wild and Wildlife Conservation Society to M. Di Bitetti and A. Paviolo. We thank Administración de Parques Nacionales and Dirección de Recursos Naturales de La Pampa for research permits.

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