Journal for Nature Conservation 31 (2016) 9–15

Contents lists available at ScienceDirect

Journal for Nature Conservation

journal homepage: www.elsevier.de/jnc

Puma density, habitat use and conflict with humans in the Argentine Chaco

Verónica A. Quiroga[a,b,*], Andrew J. Noss[c], Agustín Paviolo[a,b], Gabriel I. Boaglio[d], Mario S. Di Bitetti[a,b,e]

[a] Instituto de Biología Subtropical (IBS), Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET) and Universidad Nacional de Misiones (UNaM), Bertoni 85, Puerto Iguazú, Misiones CP 3370, Argentina
[b] Asociación Civil Centro de Investigaciones del Bosque Atlántico (CeIBA), Bertoni 85, Puerto Iguazú, Misiones CP 3370, Argentina
[c] Department of Geography, University of Florida, 1405 NW 38th St., Gainesville, FL, USA
[d] Instituto de Diversidad y Ecología Animal (IDEA), Universidad Nacional de Córdoba (UNC), Av. Vélez Sarsfield 299, Córdoba Capital, Córdoba CP 5000, Argentina
[e] Facultad de Ciencias Forestales, UNaM, Bertoni 124, Eldorado, Misiones CP 3380, Argentina

ARTICLE INFO

Article history:
Received 27 September 2015
Received in revised form 22 February 2016
Accepted 23 February 2016

Keywords:
Camera-trap
Hunting
Livestock
Occupancy

ABSTRACT

The puma Puma concolor is the most widely distributed felid in the Americas. Although it utilizes human-modified landscapes, its extensive territorial requirements, trophic needs, and real or perceived threats to livestock render the puma susceptible to conflict with humans. Our objectives were to evaluate the population density, habitat use, and puma-human conflict in the Argentine Chaco. We conducted camera-trap surveys and interviews over a three-year period, at three sites with different levels of legal protection and with different ranch outpost and livestock densities: Copo National Park (1204 trap days, 24 stations, 17 interviews, national park, lowest ranch/livestock density), Aborigen Reserve (1993 trap days, 29 stations, 13 interviews, indigenous reserve, medium ranch/livestock density) and El Cantor (2129 trap days, 35 stations, 11 interviews, no protection, highest ranch/livestock density). Puma population density was low (<1 individual/100 km^2) and we found no significant differences in puma density across the three sites. Occupancy models show a positive relationship between puma detectability and the distances from vehicle roads. Legal protection status of the área does not positively affect puma density, probably due to the large edge effect, and weak law enforcement capacity at Copo National Park. Low density of pumas at the three sites could result primarily from retaliation killing of pumas by local ranchers in response to predation on goats. Pumas in the Chaco require effectively managed protected areas, regulation of wildlife hunting and livestock management practices to minimize depredation.

© 2016 Elsevier GmbH. All rights reserved.

1. Introduction

The puma *Puma concolor* is the most wide-ranging felid in the Americas, from Canada in North America to Patagonia in South America (Currier, 1983; Shaw, Beier, Culver, & Grigione, 2007). The species is relatively tolerant to anthropogenic disturbance and maintains populations in some human-modified landscapes (De Angelo, Paviolo, & Di Bitetti, 2011; Haines, 2006). However, similar to other large carnivores, individual and population fitness is weakened as human disturbance reduces natural prey availability and fragments suitable habitat, forcing pumas to increase their already extensive territorial requirements and cross patches of unsuitable habitat (Gittleman & Harvey, 1982; Ripple et al., 2014; Wilmers et al., 2013). As a top predator, the puma also enters into conflicts with livestock owners, and is persecuted because of its perceived or actual predation of livestock (Kissling, Fernandez, & Paruelo, 2009; Soto-Shoender & Giuliano, 2011). At the same time, the puma is valued as a trophy, and direct hunting pressure is one of its principal conservation threats across its range (Carvalho & Pezzuti, 2010; Mosa & Goytia, 2004; Paviolo, Di Blanco, De Angelo, & Di Bitetti, 2009).

The implementation of protected areas is one of the most widespread strategies for the conservation of biodiversity. How-

* Corresponding author at:, Instituto de Biología Subtropical (IBS), Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET) and Universidad Nacional de Misiones (UNaM), Bertoni 85, Puerto Iguazú, Misiones CP 3370, Argentina.
E-mail addresses: veroquiroga@gmail.com, veroquiroga@hotmail.com (V.A. Quiroga), anoss@ufl.edu (A.J. Noss), paviolo4@gmail.com (A. Paviolo), gabrielboaglio@yahoo.com.ar (G.I. Boaglio), dibitetti@yahoo.com.ar (M.S. Di Bitetti).

http://dx.doi.org/10.1016/j.jnc.2016.02.004
1617-1381/© 2016 Elsevier GmbH. All rights reserved.

ever, if the protected areas are not correctly designed and implemented they may be ineffective in conserving populations of large carnivores. Home ranges of resident carnivores often extend beyond the edges of protected areas, where they suffer human-induced mortality (Balme, Slotow, & Hunter, 2010; Woodroffe & Ginsberg, 1998). This "edge effect" could drive important changes in the abundance and population dynamics of carnivores inside protected areas (Balme et al., 2010; Newby et al., 2013; Revilla, Palomares, & Delibes, 2001). In addition, many countries lack the resources to fully implement legally protected areas, thereby diminishing biodiversity conservation outcomes. In areas where poaching is widespread and law enforcement capacity is scarce, puma densities can be significantly reduced (Paviolo et al., 2009).

Poaching or hunting not only can affect population numbers, but also can have an important impact on carnivore behavior (Newby et al., 2013; Ordiz, Støen, Delibes, & Swenson, 2011; Ordiz et al., 2012; Paviolo et al., 2009; Valeix, Hemson, Loveridge, Mills, & Macdonald, 2012). The "landscape of fear" phenomenon was originally described for herbivores that tried to avoid natural predators by reducing their use of areas with high predation risk (Laundré, Hernandez, & Anteldorf, 2001). This hypothesis was tested subsequently in other species and systems, confirming that carnivores also change their activity patterns, movement patterns, and habitat use in high-risk areas (Ordiz et al., 2011, 2012; Paviolo et al., 2009; Valeix et al., 2012).

The Chaco is the second largest eco-region of South America after the Amazon, and the largest dry forest in the world (Morello & Adámoli, 1974; Morello, Rodríguez, & Silva, 2009). Jaguars (*Panthera onca*) and pumas are the top predators in the region, and were originally distributed throughout the Chaco. But the jaguar population has been reduced drastically by hunting and habitat loss, virtually disappearing in the southern part of the eco-region, in the Argentine Chaco (Quiroga, Boaglio, Noss, & Di Bitetti, 2014). Albeit with a higher tolerance, we expect the puma to react in a similar way as the jaguar to human disturbance (Currier, 1983; De Angelo et al., 2011). The objective of this study was to evaluate puma population density, habitat use and puma-human conflict in the Argentine semi-arid Chaco at three sites across a gradient of legal protection status and human disturbance.

2. Materials and methods

2.1. Study area

The semi-arid Chaco is located in the central part of the eco-region and includes parts of Argentina, Paraguay and Bolivia. The portion in Argentina covers approximately 270,000 km^2 and is characterized by extensive plains of dry forests dominated by red quebracho (*Schinopsis lorentzii*), white quebracho (*Aspidosperma quebracho-blanco*), palosanto (*Bulnesia sarmientoi*), and mistol (*Ziziphus mistol*). These canopy trees reach 18 to 20 m in height. The dense shrub understory, from 1 to 10 m high, is dominated by species of the Capparidaceae family and by thorny species like *Acacia praecox* and *Celtis pallida* (Tálamo & Caziani, 2003). The climate is markedly seasonal, with a mean annual temperature of 24 °C and annual rainfall between 400 and 800 mm, concentrated from October to April. Three rivers traverse the semiarid Argentine Chaco from northwest to southeast, while the remainder of the region is devoid of permanent water sources—giving the central portion of region its name of "Impenetrable"—with the exception of artificial ponds constructed for livestock (Caziani et al., 2003).

The region was colonized in the early 20th century by "criollos" who settled in isolated ranch outposts (permanent settlements with 1–5 family houses, livestock corrals but otherwise unfenced, and boreholes), 3–15 km apart from each other. The settlers established extensive cattle ranching systems and today raise goats (10–200 animals per outpost) and cows. Goats are enclosed in corrals only at night and by day range freely, susceptible to puma predation. Wildlife hunting is widespread, both by local residents and by hunters from nearby towns (Altrichter, 2006).

We compared puma population density, habitat use and puma-human conflict across three sites that vary in legal protection status as well as in ranch outpost and livestock density (Fig. 1). Within each site, hunting and livestock pressures are associated with the proximity of ranch outposts and roads, which provide access to the forest by people and livestock.

1) Copo National Park (1180 km^2): this site has the highest legal protection level, with four park rangers (1 park ranger/295 km^2) responsible for anti-poaching and other activities within the park. Several small human settlements exist near the Park borders, with a ranch density of 0.4 outposts/100 km^2. Livestock from neighboring ranch outposts enters the Park, but the livestock burden is relatively low in comparison to the other sites (71% of camera trap stations with photos of cows). Lacking roads and trails, the interior portion of Copo National Park is inaccessible to hunters. However, two roads constitute the northern and eastern boundaries of the Park. We did not quantify the frequency, but commonly observed hunters along these boundaries. The camera trap survey covered 367 km^2 in the northern portion of the Park, including both internal areas (i.e., inaccessible to poachers) and edges.
2) The Aborigen Reserve (2500 km^2): although it is categorized as an indigenous Reserve, no indigenous people reside inside its boundaries. It is sparsely populated by criollos (0.8 outposts/100 km^2), and has an intermediate livestock burden relative to the other two survey sites (93% of camera trap stations with photos of cows). The Reserve has no game rangers and no anti-poaching activities. Three roads cross the Reserve and facilitate access by hunters. The camera trap survey covered 455 km^2 in the center of the Reserve.
3) El Cantor (1966 km^2): this site is not legally protected, and has no game rangers nor anti-poaching activities. The resident criollos hunt. The cattle stocking rate is the highest of the three sites (100% of camera trap stations with photos of cows), and cattle have been established the longest here. The density of ranches is also the highest, at 1.3 outposts/100 km^2. Five roads cross the area and facilitate access by hunters. The camera trap survey covered 363 km^2 in the center of El Cantor.

The percentage of stations with presence of cows varies significantly among sites (X-squared = 13.71, df = NA, p-value = 0.001), and is lowest in Copo National Park. In the three sites the number of goats is proportional to the number of cattle. However, goats rarely move further than 2 km away from the ranch outposts, and did not use the trails, therefore we rarely recorded them during the camera-trap surveys. Nevertheless, they may attract pumas to the posts and are occasionally preyed upon by pumas. In the case of Copo National Park the goats rarely enter the park, but their presence is conspicuous near its borders.

2.2. Camera-trap surveys

We undertook camera-trap surveys during three consecutive years (2008–2010), during a three-month period each year (between June and November according to the site). At each site we installed 24–35 camera-trap stations separated by an average of 3 km, using two cameras, 30 cm above the ground, facing each other across foot trails or dirt roads in each station. We used a pool of analog 35 mm film cameras (Deer Cam® Model DC 300, Cam Trakker®, and Leaf River Trail Scan® Model C-1) at all three sites, supple-

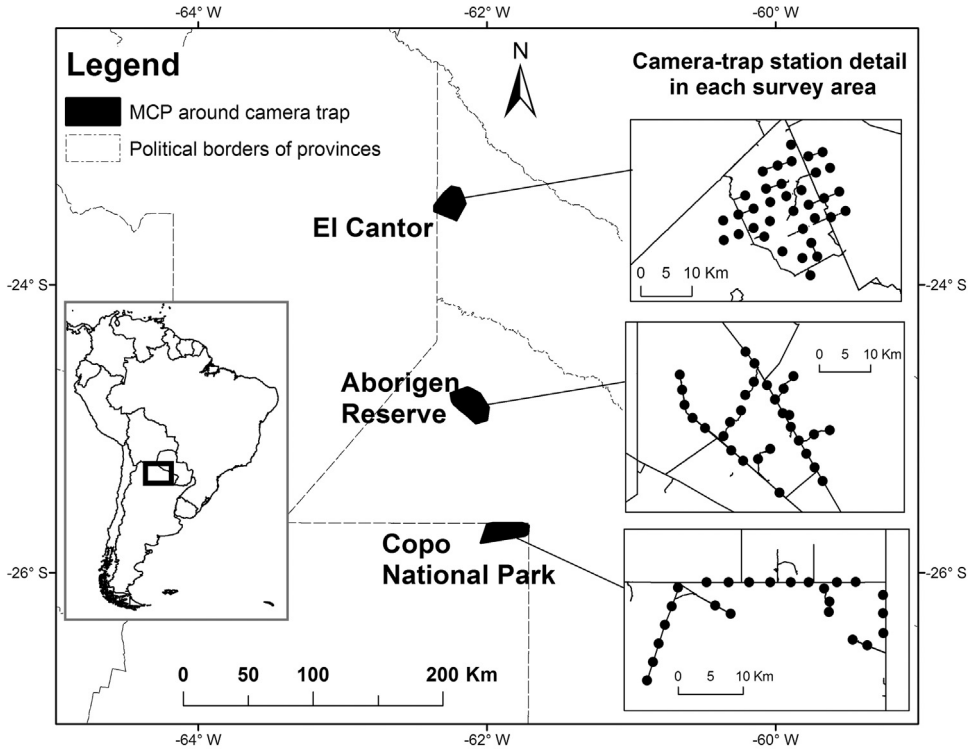

Fig. 1. The three study sites in the Argentine semi-arid Chaco.

mented by digital (Cuddeback® Expert) cameras at El Cantor. In each survey the camera models were interspersed across the survey area in order to avoid any biases that could result from differing sensibility of the camera models. Camera-traps were active 24 h a day, with a minimum one-minute delay between consecutive photos. Sensitivity was set at medium or high depending on camera model and previous experience. Camera-traps were active for an average of 58 days at each site (Table 1). We checked the cameras weekly to change film, batteries and memory cards as needed.

We used the camera-trap photographs to confirm puma presence, to determine the number of individuals, and to estimate puma density according to the captures and recaptures of the distinct individuals. We used the same photos in combination with occupancy models (MacKenzie et al., 2002) to estimate the proportion of the study area utilized by pumas, and the detectability of the species relative to environmental variables indicating human disturbance. In the case of species with spotted pelts, like the jaguar, individuals can be distinguished by spot patterns (Karanth, 1995). In the case of pumas, individuals are more difficult to distinguish, but can also be identified following established protocols (Kelly et al., 2008; Paviolo et al., 2009; Rich et al., 2014). Two investigators worked independently to identify the individual pumas in the photos and in turn to estimate population density for each site. They considered only adult individuals, and used unique marks such as the shape and color of the tail and its tip, how the tail is carried, scars, and spots on the inside of the legs (Kelly et al., 2008; Rich et al., 2014). We used the presence or absence of scrotum to define the sex of the photographed individuals.

2.3. Density estimations using capture-recapture models

To estimate puma population density, we applied both traditional (Karanth & Nichols, 2002), as well as spatially-explicit (Royle, Karanth, Gopalaswamy, & Kumar, 2009), capture-recapture models. We used both approaches in order to be able to compare our density estimates with previous studies elsewhere across the continent. Both models use the number of individuals identified and the capture-recapture history at each camera-trap station. In the traditional models, we first estimated puma abundance in the survey area using the software CAPTURE 2 (version <050810.1025> by Jim Hines; http://www.mbr-pwrc.usgs.gov), and in turn estimated the effective survey area by applying a buffer around the camera-trap polygon equivalent to the Mean Maximum Distance Moved (MMDM) by all individuals captured in more than one station (Karanth, 1995; Karanth & Nichols, 2002; Kelly et al., 2008; Maffei, Noss, Silver, & Kelly, 2011). Consistent with most other studies on large carnivores, we used the heterogeneity model (M_h) to estimate abundance, as this model best approximates the species' behavior (Karanth, 1995), and we used the jackknife estimator, which is more robust than other estimators (Silver et al., 2004). Spatially-explicit capture-recapture (SECR) models estimate population density directly by using the capture-recapture history in combination with the spatial distribution of the captures and recaptures (Noss et al., 2012; Reppucci, Gardner, & Lucherini, 2011; Royle et al., 2009; Singh, Gopalaswamy, Royle, Kumar, & Karanth, 2010). We used the software SPACECAP (version 1.0.1), which applies a Bayesian modeling framework (Gopalaswamy et al., 2012). In

Table 1
Camera trap survey effort for pumas at three Argentine semi-arid Chaco sites.

Site	Survey dates	N° of stations	Trap-days (systematic survey)	Total trap-days (including pilot)	Mean distance among cameras (km ± SD)
El Cantor	1/Jul/2010 to 9/Sep/2010	35	1820	2129	2.99 ± 0.32
Aborigen Reserve	23/Jun/2008 to 7/Sep/2008	29	1624	1937	3.04 ± 0.98
Copo National Park	4/Sep/2009 to 19/Nov/2009	24	792	1204	2.85 ± 0.65

accordance with these previous studies, for each area we ran 100,000 iterations. To define the extent of the state space for the analysis we selected an area that included all the cameras plus a buffer area of 50 km. That distance is approximately 10 times the average radius of home ranges for four radio-collared male pumas in the Paraguayan Chaco (the closest region for which such information is available, McBride, 2009). The probability of recording an animal from outside this area during the survey period is very low (Gopalaswamy et al., 2012). We applied a standard pixel area of 1 km^2 for each potential activity center; this is a reasonable size to ensure many potential activity centers per home range, as well as reasonable computational times (Gopalaswamy et al., 2012). Camera trap data confirm that pumas do move large distances across the study sites, therefore a pixel smaller than 1 km^2 would be unnecessary. We based the augmentation values (150–300 individuals) on the number of puma observations obtained in each area, adjusted in accordance with the density plot for ψ and N. We based the burn-in period (20,000–35,000 iterations) on the values of the Geweke test (with a z-score between −1.6 and +1.6.) (Gopalaswamy et al., 2012). For each estimation, we ran the models 2–4 times in order to make the appropriate adjustments for the final analysis.

2.4. Occupancy models

Occupancy models can be used to reveal what factors affect, positively or negatively, site occupancy or proportion of sites used (ψ), modeling the effects of these factors according to the species' detection probability (p) (MacKenzie et al., 2002, 2006). In our analyses we estimate the proportion of sites used by pumas (with the software PRESENCE version 4.4; Hines, 2006). We considered the 88 camera-trap stations across the three surveys to be distinct survey points, and we assumed no temporal changes in population abundance among sites. During the three-year study period no unusual climatic or environmental events occurred in the study area. For each station we grouped the maximum number of 64 survey days in eigth capture occasions of eigth days each. If a station was active fewer days overall, then we used the greatest multiple of eigth possible, and eliminated the extra days. We ranked models by their Akaike Information Criteria (AIC) weights. Instead of choosing the single highest-ranked model, we estimated an average of the highest-ranked models (those with AIC weights 10% or greater of the weight of the highest-ranked model) (MacKenzie et al., 2006). We evaluated the effects of three co-variables on the proportion of sites used (ψ) or detectability (p) of pumas:

(1) The distance (km, range 0.5–13.8) to the nearest ranch outpost. We expected this distance to be positively related to ψ and p, because of direct puma hunting by ranch inhabitants, and/or the combined disturbance effects of the ranch—including human presence, dogs, cattle, goats, and vegetation modification (Altrichter, 2006).
(2) The distance (km, range 0–15) to the nearest vehicle road. We expected that ψ and p would vary positively with this distance, because of the hunting pressure concentrated along vehicle roads (e.g., Boas Goulart et al., 2008). For these two co-variables, distance to vehicle road and distance to nearest ranch outpost, we applied one-tailed statistical tests because our hypothesis was directional.
(3) The type of trail/road (vehicle roads, abandoned roads and narrow footpaths) where the camera-trap station was installed. There is a generalized preference of felids for using roads or trails rather than bushwhacking (Cusack et al., 2015), and they are known to prefer unpaved roads over narrow footpaths. We therefore predicted this co-variable would affect p because the pumas, when present, would more frequently use vehicle roads or abandoned roads than footpaths (e.g., Di Bitetti, Paviolo, & De Angelo, 2006; Di Bitetti, De Angelo, Paviolo, & Di Blanco, 2008).

Table 2
Comparison of 95% confidence intervals for density estimates (individuals per 100 km^2) of pumas using traditional and spatially-explicit capture-recapture models, at three Argentine semi-arid Chaco sites.

Site	Traditional model		Spatially-explicit capture-recapture model	
	Investigator 1	Investigator 2	Investigator 1	Investigator 2
El Cantor	0.51–0.92	0.59–1.11	0.08–0.59	0.09–0.75
Aborigen Reserve	0.51–0.97	0.44–1.10	0.27–1.26	0.08–1.05
Copo National Park	0.31–0.84	0.17–0.45	0.08–0.57	0.10–0.27

To build the models we tested the influence of the three variables at the same time on either ψ or p.

Wild prey availability was not considered as an influential covariate in our analysis since the most important puma's prey (e.g., *Mazama gouazoubira*, *Sylvilagus brasiliensis*, *Dolichotus salinicola*, *Tolypeutes matacus*, among others) are relatively abundant in the study sites (Quiroga, V. A., 2013). Thus, we do not consider prey availability to be an important and limiting factor for pumas in the study areas, and therefore was not included in the analysis.

2.5. Interviews

During the systematic camera-trap surveys we conducted 41 informal semi-structured interviews with rural residents of the three surveyed areas: 17 in Copo National Park, 13 in Aborigen Reserve and 11 in El Cantor. All the people interviewed were adult male and had livestock of their own. During the interviews we asked about poaching of pumas and conflicts due to predation on livestock during the previous year, potential causes of conflicts, and solutions to solve the conflicts. The main goals of the interviews were to generate information about the frequency of puma poaching in the different areas and help us understand the level of puma-human conflict.

3. Results

3.1. Puma population density

We identified, from the camera trap photos, between 10 and 12 pumas at Copo National Park, between 7 and 8 at the Aborigen Reserve, and 9 at El Cantor. We recorded adult males and females as well as kittens and/or juveniles at all three sites. We recorded between 4 and 5 females, between 5 and 6 males and 1 unsexed individual at Copo National Park; 3 females and between 4 and 5 males at the Aborigen Reserve; and between 4 and 5 females and between 3 and 5 males at El Cantor. Although the two investigators did not coincide in the number of individuals identified at the two first sites, the density estimations using traditional models (and MMDM) as well as SECR models did not vary significantly between the two investigators (95% confidential intervals overlapped). Also, the densities estimates were not statistically different (95% confidential intervals overlapped) between the site with legal protection (Copo National Park) and the sites without legal protection (Table 2).

3.2. Occupancy models

Using the model in which all sites had the same probability of species presence, and in which the detection probability was constant across time and sites [$\psi(.)$; $p(.)$], the proportion of sites used by pumas ($\psi \pm$ SE) across the entire study area was 0.75 ± 0.07,

Table 3
Occupancy models for puma in the Argentine Chaco ranked by their Akaike Information Criteria (AIC), considering only models with AIC weights >10% of the highest ranked model.

Model	AIC	ΔAIC	AIC wgt	no.Par.
ψ(dis ranch, dis road), p(dis ranch, dis road)	524.05	0	0.2891	6
ψ(dis ranch, dis road), p(trail, dis ranch, dis road)	525.45	1.4	0.1435	7
ψ(.), p(dis road)	526.25	2.2	0.0962	3
ψ(.), p(trail, dis road)	526.29	2.24	0.0943	4
ψ(dis ranch, dis road), p(dis road)	526.77	2.72	0.0742	5
ψ(dis ranch, dis road), p(trail, dis road)	526.98	2.93	0.0668	6
ψ(.), p(dis road, dis ranch)	527.4	3.35	0.0541	4
ψ(dis ranch), p(trail, dis road)	527.84	3.79	0.0435	5
ψ(dis ranch), p(dis road)	527.96	3.91	0.0409	4
ψ(.), p(trail, dis ranch, dis road)	528.06	4.01	0.0389	5
ψ(dis ranch), p(dis ranch, dis road)	528.32	4.27	0.0342	5
ψ(dis ranch), p(trail, dis ranch, dis road)	529.11	5.06	0.023	6

Table 4
Parameter estimates of the average model. The weighted averaged model is estimated using the highest-ranked model and models with AIC weights 10% or greater of the weight of the highest-ranked one.

	Beta model averaging	SE	95% confidence interval	
			Superior	Inferior
Site use (ψ)				
Intercept estimate	3.27	2.41	8.40	−1.86
Distance to the nearest ranch	2.81	2.55	6.71	−1.10
Distance to the nearest road	−1.93	1.64	0.58	−4.44
Detectability (p)				
Intercept estimate	−1.48	1.42	1.54	−4.50
Distance to the nearest ranch	−0.18	0.18	0.11	−0.46
Distance to the nearest road	0.54	0.16	0.79	0.29
Type of trail	−0.06	0.11	0.17	−0.30

with a 95% confidence interval of 0.59–0.86. The average of the highest-ranked models indicates that the only parameter for which the estimated 95% confidence interval did not include 0 was the β for detection probability (p) of pumas as a function of the distance to the nearest road (Tables 3 and 4).

3.3. Puma-livestock conflict and puma retaliation killing

In Copo National Park all 17 interviewees reported puma predation on goats, and 8 (47% of the interviewees) admitted they had killed pumas in the past year. Of 13 people interviewed at the Aborigen Reserve, only one said he had had no puma predation on livestock in recent years, though he knew pumas had been attacking goats on his neighbor's ranch. The other 12 interviewees confirmed heavy losses by pumas, and at least 7 people (58% of the interviewees) had killed a puma in the past year. Similarly, in El Cantor all 11 interviewees reported puma predation on goats, and at least 5 of them (42% of the interviewees) had tried to kill pumas in the past year, but reportedly without success. At all three sites, 100% of interviewees affirmed that predation on goats was frequently by female pumas teaching their young to hunt, and that conflicts were more common in the dry season (May–October). All interviewees also affirmed that the predation problem can be greatly reduced or even eliminated by using well-trained shepherd dogs to tend the goat herds and by enclosing the goats in corrals at night. However, the interviewees explained that dogs are useless if not appropriately trained. The few people in the region who know how to train shepherd dogs are old women who have inherited this skill from their mothers or grandmothers. As for night-time corrals, 85% of the interviewees said they lack the time or help to build and maintain them, in addition to all their domestic and ranch duties.

4. Discussion

Puma density estimates were very low across the three sites, and our surveys could not demonstrate a statistically significant effect of legal protection status on density. It is important to note, however, that the camera trap survey in Copo National Park may be capturing important edge effects because it covered only the northern site of the Park, where roads constitute two of the boundaries of the protected area. In addition, people living in the 10 ranch outposts neighboring the Park frequently kill pumas in response to attacks on livestock, as occurs within the other two survey areas. Individual pumas utilize extensive territories (Beier, 1993; Shaw et al., 2007; Smallwood, 1997), thus perhaps even those individuals whose territories encompass the interior of the Copo National Park move in and out of the park, thereby exposing themselves to the same threats (for instance, road-based hunters) facing pumas at the other two sites. Human-induced mortality at the edges of protected areas can reduce the densities of carnivores, and the negative effect may extend well inside protected areas (Balme et al., 2010; Davis, Kelly, & Stauffer, 2011; Revilla et al., 2001; Woodroffe & Ginsberg, 1998). Our study suggests this might be occurring in Copo National Park. On the other hand, is important to note that the small sample size (only three areas) of our study may also be influencing the pattern we detected, and therefore the results should be carefully interpreted.

Other studies undertaken across a variety of eco-regions and conservation contexts reveal no consistent relationship between pumas and human disturbance (Davis et al., 2011; De Angelo et al., 2011; Foster, Harmsen, & Doncaster, 2010; Negrões et al., 2010; Payán Garrido, 2009; Sollmann et al., 2012). We found only one variable associated with human disturbance, distance to roads, that affects puma detection probability (p) in the Argentine Chaco. We expected that pumas would avoid ranch outposts, because pumas are frequently killed in retaliation for livestock losses, but our data did not support this hypothesis. Although the ranches are dangerous places to be avoided, perhaps pumas are drawn to the abundant easy prey (goats) that concentrate around ranch outposts. Other large carnivores face similar opposing pressures (Ordiz et al., 2011, 2012; Valeix et al., 2012). In Botswana, lions do not avoid cattle posts, but use these areas at times when humans are least active, to minimize the chance of encounters (Valeix et al., 2012). Similarly, brown bears in Scandinavia do not shift their ranges when the hunting season starts, but change their movement patterns to avoid encounters with people (Ordiz et al., 2012). We also expected that pumas would avoid roads as risky places that facilitate access for hunters from nearby cities and towns (Mosa & Goytia, 2004). On the other hand, unpaved roads also make walking easier for pumas, compared to traversing forest or brush, and big cats at many sites seem to prefer such roads (Blake & Mosquera, 2014; Cusack et al., 2015; Di Bitetti, Paviolo, & De Angelo, 2014; Harmsen, Foster, Silver, Ostro, & Doncaster, 2009; Rabinowitz & Nottingham, 1986). In this case our data do support our hypothesis, thus pumas' wariness of humans must outweigh the benefit of walking on roads at our study sites, either because the risk from humans is especially high in the Argentine Chaco, or the abundant cattle open numerous trails that pumas also use, or a combination of the two.

According to the interviewees, puma predation on goats is very common, especially during the dry season (May–October). Although they know management measures that can reduce predation (shepherd dogs and night-time enclosures), time and resource limitations prevent livestock owners from adopting them. As a result, retaliation killing of pumas because of predation on livestock in criollo ranch outposts is very high, and is probably one of the main factors causing low puma population density in this region, as elsewhere across the puma's range (Conforti & Cascelli de Azevedo, 2003; Inskip & Zimmermann, 2009; Kissling et al., 2009;

Mazzolli, Graipel, & Dunstone, 2002; Novack, Main, Sunquist, & Labisky, 2005; Perovic, 2003).

In some well-protected regions puma densities are much higher: 1.55–2.89 pumas/100 km^2 in Iguazú in the Atlantic Forest of Argentina, 7.99/100 km^2 in Ravelo in the Bolivian Chaco, and 3.42/100 km^2 in Belize. The low puma densities in the Argentine Chaco are similar to other areas of high hunting pressure in the Americas: 0.31–0.74/100 km^2 in Yabotí in the Atlantic Forest of Argentina and 0.36/100 km^2 in Cerro in the Bolivian Chaco (Kelly et al., 2008; Mazzolli, 2010; Negrões et al., 2010; Noss et al., 2012; Paviolo et al., 2009; Soria-Díaz, Monroy-Vilchis, Rodríguez-Soto, Zarco-González, & Urios, 2010). Although we did not find an effect on puma density of legal protection status across our sites, we consider that protected areas are essential to puma conservation. However, existing protected areas such as Copo National Park must be managed more effectively, with sufficient staff and resources to implement essential conservation measures. These measures must include wildlife hunting regulation and a reduction of puma-human conflicts in the neighboring properties by improved livestock management practices, especially for goats.

These management and conservation measures must also be implemented on communal and indigenous lands such as the Aborigen Reserve, as well as on private lands. Furthermore, zoning plans exist to conserve native forests and effective biological corridors where puma and human activities can coexist, allowing pumas to move safely among protected areas. These zoning plans must be implemented and must include the creation of new effectively managed protected areas. These recommendations echo those urgently required to protect jaguars in the region (Quiroga et al., 2014); both pumas and jaguars (and several others through trophic cascades) will only survive in the Argentine Chaco if these recommendations are adopted.

Acknowledgments

We thank the volunteers who helped with field work; the Agency of Wildlife, Parks and Ecology, Chaco Province; the Ministry of Production and Environment, Formosa Province; Copo National Park, the National Parks Administration; the National University, Córdoba; the National Wildlife Service, National Environment and Sustainable Development Secretariat. Financial and logistical support was provided by CONICET-Argentina, Jaguar Conservation Program-WCS, Rufford Small Grants Foundation, Cleveland Metroparks Zoo and Cleveland Zoological Society, Mohamed bin Zayed Species Conservation Fund, Idea Wild, Elé Project, Stephen F. Austin State University, Yaguareté Project Misiones and Tapir Project Salta. We thank Pablo Perovic, Ricardo Banchs, Gustavo Porini, Adrián Díaz, Daniel Scognamillo, Andrés Ravelo, Peter Feinsinger, Yamil Di Blanco, Paula Cruz, Carlos De Angelo and Susan Walker for their support and advice at different stages of this project. We particularly thank Yamil Di Blanco for his collaboration in identifying individual pumas.

References

Altrichter, M. (2006). Wildlife in the life of local people of the semiarid Argentine Chaco. *Biodiversity and Conservation*, *15*, 2719–2736.

Balme, G. A., Slotow, R., & Hunter, L. T. B. (2010). Edge effects and the impact of non-protected areas in carnivore conservation: leopards in the Phinda–Mkhuze Complex, South Africa. *Animal Conservation*, *13*, 315–323.

Beier, P. (1993). Determining minimum habitat areas habitat corridors for cougars. *Conservation Biology*, *7*(1), 94–108.

Blake1, J. G., & Mosquera, D. (2014). Camera trapping on and off trails in lowland forest of eastern Ecuador: does location matter? *Mastozoología Neotropical*, *21*(1), 17–26.

Boas Goulart, F. V., Cáceres, N. C., Greipel, M. E., Tortato, M. A., Rohling Ghizoni, I., Jr., & Rodrigues Oliveira-Santos, L. G. (2008). Habitat selection by large mammals in a southern Brazilian Atlantic forest. *Mammalian Biology*, *74*, 182–190.

Carvalho, E. A. R., Jr., & Pezzuti, J. C. B. (2010). Hunting of jaguars and pumas in the Tapajós–Arapiuns Extractive Reserve, Brazilian Amazonia. *Oryx*, *44*(4), 610–612.

Caziani, S., Trucco, C. E., Perovic, P. G., Talamo, A., Derlindati, E. J., & Adámoli, J. (2003). *Línea de base y programa de monitoreo de biodiversidad del Parque Nacional Copo*. Argentina: Administración de Parques Nacionales. Proyecto de Conservación de la Biodiversidad-BIRF/GEF TF 028372-AR

Conforti, V. A., & Cascelli de Azevedo, F. C. (2003). Local perceptions of jaguars (*Panthera onca*) and pumas (*Puma concolor*) in the Iguaçu Nacional Park, south Brazil. *Biological Conservation*, *111*, 215–221.

Currier, M. J. P. (1983). Felis concolor. *Mammalian Species*, *200*, 1–7.

Cusack, J. J., Dickman, A. J., Rowcliffe, J. M., Carbone, C., Macdonald, D. W., & Coulson, T. (2015). Random versus game trail-based camera trap placement strategy for monitoring terrestrial mammal communities. *PLoS One*, *10*(5), e0126373. http://dx.doi.org/10.1371/journal.pone.0126373

Davis, M. L., Kelly, M. J., & Stauffer, D. F. (2011). Carnivore co-existence and habitat use in the Mountain Pine Ridge Forest Reserve, Belize. *Animal Conservation*, *14*, 56–65.

De Angelo, C., Paviolo, A., & Di Bitetti, M. (2011). Differential impact of landscape transformation on pumas (*Puma concolor*) and jaguars (*Panthera onca*) in the Upper Paraná Atlantic Forest. *Diversity and Distributions*, 1–15.

Di Bitetti, M. S., Paviolo, A., & De Angelo, C. (2006). Density, habitat use and activity patterns of ocelots (*Leopardus pardalis*) in the Atlantic Forest of Misiones, Argentina. *Journal of Zoology*, *270*, 153–163.

Di Bitetti, M. S., De Angelo, C., Paviolo, A., & Di Blanco, Y. (2008). Local and continental correlates of the abundance of a neotropical cat, the ocelot (*Leopardus pardalis*). *Journal of Tropical Ecology*, *24*(2), 189–200.

Di Bitetti, M. S., Paviolo, A., & De Angelo, C. (2014). Camera trap photographic rates on roads vs. Off roads: location does matter. *Mastozoología Neotropical*, *21*(1), 37–46.

Foster, R. J., Harmsen, B. J., & Doncaster, C. P. (2010). Habitat use by sympatric jaguars and pumas across a gradient of human disturbance in Belize. *Biotropica*, *42*(6), 724–731.

Gittleman, J. L., & Harvey, P. H. (1982). Carnivore home-range size: metabolic needs and ecology. *Behavioral Ecology and Sociobiology*, *10*, 57–63.

Gopalaswamy, A. M., Royle, J. A., Hines, J. E., Singh, P., Jathanna, D., Samba Kumar, N., et al. (2012). Program SPACECAP: software for estimating animal density using spatially explicit capture–recapture models. *Methods in Ecology and Evolution*, *3*(4), 1–6.

Haines, A. M. (2006). Is there competition between sympatric jaguar *Panthera onca* and puma *Puma concolor*? *Acta Zoológica Sinica*, *52*(6), 1142–1147.

Harmsen, B. J., Foster, R. J., Silver, S. C., Ostro, L. E. T., & Doncaster, C. P. (2009). Spatial and temporal interactions of sympatric jaguars (*Panthera onca*) and pumas (*Puma concolor*) in a neotropical forest. *Journal of Mammalogy*, *90*, 612–620.

Hines, J. E. (2006). *PRESENCE 2-software to estimate patch occupancy and related parameters*. USGS-PWRC. http://www.mbr-pwrc.usgs.gov/software/presence.html/

Inskip, C., & Zimmermann, A. (2009). Human-felid conflict: a review of patterns and priorities worldwide. *Oryx*, *43*(1), 18–34.

Karanth, K. U. (1995). Estimating tiger *Panthera tigris* populations from camera – trap data using capture – recapure models. *Biological Conservation*, *71*, 333–338.

Karanth, K. U., & Nichols, J. D. (2002). *Monitoring tigers and their prey: a manual for researchers, managers and conservationists in tropical Asia*. Bangalore, India: Centre for Wildlife Studies.

Kelly, M. J., Noss, A. J., Di Bitetti, M. S., Maffei, L., Arispe, R., Paviolo, A., et al. (2008). Estimating puma densities from camera trapping across three study sites: Bolivia, Argentina, Belize. *Journal of Mammalogy*, *89*(2), 408–418.

Kissling, D. W., Fernandez, N., & Paruelo, J. M. (2009). Spatial risk assessment of livestock exposure to pumas in Patagonia, Argentina. *Ecography*, *32*, 807–817.

Laundré, J. W., Hernandez, L., & Anteldorf, K. B. (2001). Wolves, elk, and bison: reestablishing the landscape of fear in Yellowstone National Park, U.S.A. *Canadian Journal of Zoology*, *79*, 1401–1409.

McBride, R. (2009). *Project jaguar. Final report 2002–2009*. pp. 55. Faro Moro Eco Research; Moises Bertoni Fundation and Paraguayan Ministy of Environment (SEAM).55.

MacKenzie, D. I., Nichols, J. D., Lachman, G. B., Droege, S., Royle, A. J., & Langtimm, C. A. (2002). Estimating site occupancy rates when detection probabilities are less than one. *Ecology*, *83*(8), 2248–2255.

MacKenzie, D. I., Nichols, J. D., Royle, J. A., Pollock, K. H., Hines, J. E., & Bailey, L. L. (2006). *Occupancy estimation and modeling: inferring patterns and dynamics of species occurrence*. San Diego, USA: Elsevier.

Maffei, L., Noss, A. J., Silver, S., & Kelly, M. J. (2011). Abundance/density case study: jaguars in the Americas. In A. F. O'Connell, J. D. Nichols, & U. K. Karanth (Eds.), *Camera traps in animal ecology: methods and analyses* (pp. 119–144). Tokyo, Japan: Springer Tokyo, Inc.

Mazzolli, M. (2010). Mosaics of exotic forest plantations and native forests as habitat of pumas. *Environmental Management*, *46*, 237–253.

Mazzolli, M., Graipel, M. E., & Dunstone, N. (2002). Mountain lion depredation in southern Brazil. *Biological Conservation*, *105*, 43–51.

Morello, J., & Adámoli, J. (1974). *Las grandes unidades de vegetación y ambiente del Chaco argentino. Segunda Parte: Vegetación y ambiente de la Provincia del Chaco*. INTA Serie Fitogeográfica 13.

Morello, J. H., Rodríguez, A. F., & Silva, M. (2009). Clasificación de ambientes en áreas protegidas de las ecorregiones del Chaco húmedo y Chaco seco. In J. H.

Morello, & A. F. Rodríguez (Eds.), *El Chaco sin bosques: la Pampa o el desierto del futuro* (pp. 53–89). Buenos Aires: Orientación Gráfica Editora.
Mosa, S. G., & Goytia, M. (2004). Evaluación de la caza recreativa sobre la fauna silvestre en las provincias de Salta y Jujuy, Argentina. In *Memorias: manejo de fauna silvestre en amazonía y latinoamérica. VI congreso* (pp. 457–471).
Negrões, N., Sarmento, P., Cruz, J., Eira, C., Revilla, E., Fonseca, C., et al. (2010). Use of camera-trapping to estimate puma density and influencing factors in central Brazil. *Journal of Wildlife Management*, *74*(6), 1195–1203.
Newby, J. R., Mills, L. S., Ruth, T. K., Pletscher, D. H., Mitchell, M. S., Quigley, H. B., et al. (2013). Human-caused mortality influences spatial population dynamics: pumas in landscapes with varying mortality risks. *Biological Conservation*, *159*, 230–239.
Noss, A. J., Gardner, B., Maffei, L., Cuellar, E., Montaño, R., Romero-Muñoz, A., et al. (2012). Comparison of density estimation methods for mammal populations with camera traps in the Kaa-Iya del Gran Chaco landscape. *Animal Conservation*, *15*(3), 1–11.
Novack, A. J., Main, M. B., Sunquist, M. E., & Labisky, R. F. (2005). Foraging ecology of jaguar (*Panthera onca*) and puma (*Puma concolor*) in hunted and non-hunted sites within the Maya Biosphere Reserve, Guatemala. *Journal of Zoology*, *267*, 167–178.
Ordiz, A., Støen, O., Delibes, M., & Swenson, J. E. (2011). Predators or prey? Spatio-temporal discrimination of human-derived risk by brown bears. *Oecologia*, *166*(1), 59–67.
Ordiz, A., Støen, O., Sæbø, S., Kindberg, J., Delibes, M., & Swenson, J. E. (2012). Do bears know they are being hunted? *Biological Conservation*, *152*, 21–28.
Paviolo, A., Di Blanco, Y. E., De Angelo, C. D., & Di Bitetti, M. S. (2009). Protection affects puma abundance and activity patterns in the Atlantic Forest. *Journal of Mammalogy*, *90*(4), 926–934.
Payán Garrido, C. E. (2009). *Hunting sustainability, species richness and carnivore conservation in Colombian Amazonia. Ph.D. dissertation*. London, United Kingdom: University College London, Institute of Zoology/ZSL.
Perovic, P. (2003). *Diagnóstico del estado de conflicto jaguar/puma/actividades humanas, en el Parque Nacional Copo y zonas de amortiguamiento*. pp. 1–48. Argentina: Administración de Parques Nacionales. Proyecto de Conservación de la biodiversidad—Donación BIRF/GEF TF 028372–AR.
Quiroga, V. A., Boaglio, G. I., Noss, A. J., & Di Bitetti, M. (2014). Critical population status of the jaguar in the Argentine Chaco: camera trap surveys suggest recent collapse and imminent regional extinction. *Oryx*, *48*(1), 141–148.
Rabinowitz, A., & Nottingham, B. G., Jr. (1986). Ecology and behaviour of the jaguar (*Panthera onca*) in Belize, Central America. *Journal of Zoology*, *210*, 149–159.
Reppucci, J., Gardner, B., & Lucherini, M. (2011). Estimating detection and density of the Andean cat in the high Andes. *Journal of Mammalogy*, *92*(1), 140–147.
Revilla, E., Palomares, F., & Delibes, E. (2001). Edge-core effects and the effectiveness of traditional reserves in conservation: eurasian badgers in Doñana National Park. *Conservation Biology*, *15*(1), 148–158.
Rich, L. N., Kelly, M. J., Sollmann, R., Noss, A. J., Maffei, L., Arispe, R. L., et al. (2014). Comparing capture-recapture, mark-resight and spatial mark-resight models for estimating puma densities via camera traps. *Journal of Mammalogy*, *95*(2), 382–391.
Ripple, W. J., Estes, A. J., Beschta, R. L., Wilmers, C., Ritchie, E. G., Hebblewhite, M., et al. (2014). Status and ecological effects of the world's largest carnivores. *Science*, *343*, 1241484.
Royle, J. A., Karanth, K. U., Gopalaswamy, A. M., & Kumar, N. S. (2009). Bayesian inference in camera trapping studies for a class of spatial capture-recapture models. *Ecology*, *90*, 3233–3244.
Shaw, H. G., Beier, P., Culver, M., & Grigione, M. (2007). *Puma field guide*. The Cougar Network.
Silver, S. C., Ostro, L. E. T., Marsh, L. K., Maffei, L., Noss, A. J., Kelly, M. J., et al. (2004). The use of camera traps for estimating jaguar Panthera onca abundance and density using capture/recapture analysis. *Oryx*, *38*, 148–154.
Singh, P., Gopalaswamy, A. M., Royle, A. J., Kumar, N. S., & Karanth, K. U. (2010). *SPACECAP: a program to estimate animal abundance and density using bayesian spatially-explicit capture-recapture models (Versión 1.0.)*. pp. 1–9. Bangalore, India: Wildlife Conservation Society—India Program, Centre for Wildlife Studies.
Smallwood, K. S. (1997). Interpreting puma (*Puma concolor*) population estimates for theory and management. *Environmental Conservation*, *24*(3), 283–289.
Sollmann, R., Malzoni Furtado, M., Hofer, H., Jácomo, A. T. A., Mundim Tôrres, N., & Silveira, L. (2012). Using occupancy models to investigate space partitioning between two sympatric large predators, the jaguar and puma in central Brazil. *Mammalian Biology*, *77*, 41–46.
Soria-Díaz, L., Monroy-Vilchis, O., Rodríguez-Soto, C., Zarco-González, M. M., & Urios, V. (2010). Variation of abundance and density of *Puma concolor* in zones of high and low concentration of camera traps in Central Mexico. *Animal Biology*, *60*, 361–371.
Soto-Shoender, J., & Giuliano, W. M. (2011). Predation on livestock by large carnivores in the tropical lowlands of Guatemala. *Oryx*, *45*(4), 561–568.
Tálamo, A., & Caziani, S. M. (2003). Variation in woody vegetation among sites with different disturbance histories in the Argentine Chaco. *Forest Ecology and Management*, *184*, 79–92.
Valeix, M., Hemson, G., Loveridge, A. J., Mills, G., & Macdonald, D. W. (2012). Behavioural adjustments of a large carnivore to access secondary prey in a human-dominated landscape. *Journal of Applied Ecology*, *49*, 73–81.
Wilmers, C. C., Wang, Y., Nickel, B., Houghtaling, P., Shakeri, Y., Allen, M. L., et al. (2013). Scale dependent behavioral responses to human development by a large predator, the puma. *PLoS One*, *8*(4), e60590.
Woodroffe, R., & Ginsberg, J. R. (1998). Edge effects and the extinction of populations inside protected areas. *Science*, *5372*(280), 2126–2128.