

## Density and activity patterns of pumas in hunted and non-hunted areas in central Argentina

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### Abstract

**Context.** Hunting has demographic effects on large and medium carnivores, causing population reductions and even extinctions worldwide. Yet, there is little information on carnivore demographic parameters and spatial and temporal land-use patterns in areas experiencing sport hunting, thus hindering effective conservation plans for such areas.

**Aims.** We estimated densities and determined activity patterns of pumas (*Puma concolor*) from camera-trapping surveys in a protected area and in a game reserve with sport hunting, in the Caldén forest of central Argentina.

**Methods.** We used both non-spatial and spatial mark–resight techniques to estimate and compare puma densities and we used kernel-density estimation (KDE) techniques to analyse and compare puma activity patterns between study sites.

**Key results.** Puma densities estimated from spatial models were lower than densities estimated from non-spatial mark–resight techniques. However, estimated density of pumas in the protected area was always higher (range = 4.89–9.32 per 100 km<sup>2</sup>) than in the game reserve (range = 0.52–1.98 per 100 km<sup>2</sup>), regardless of the estimation technique used. Trapping rates for large mammal prey were similar across sites. Pumas exhibited more nocturnal behaviour and high activity peaks at 0600 hours and 1100 hours in the hunted game reserve, whereas puma activity was spread more evenly around the clock in the protected area.

**Conclusions.** The higher puma densities in the protected area reflect the potential for such areas to function as refugia in a human-dominated landscape. However, the game reserve had a lower puma density than the protected area despite high trap rates of large prey, indicating that these areas may function as attractive sinks.

**Implications.** Our results could indicate that puma sport hunting in the Caldén forest should be managed at a metapopulation, regional level, and include both no-hunting areas (protected area, as potential sources) and hunting areas (game reserves, as potential sinks). Considering that our study areas were small and that this was an unreplicated study, we urge more research to be conducted, so as to determine whether sport hunting is compatible with puma conservation in the region.

**Additional keywords:** Caldén forest, camera surveys, hunting, mark–resight, population density, *Puma concolor*.

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### Introduction

Large carnivores are widely hunted for recreation, population control and to reduce conflict with humans (Treves and Karanth 2003). Yet, both regulated and unregulated hunting have direct demographic effects, especially for large and medium-sized carnivores that have low population growth rates, and can

potentially cause population reductions and even extinctions worldwide (Woodroffe and Ginsberg 1998; Treves 2009). Additionally, hunting can have indirect effects on carnivore populations by altering behaviour (e.g. daily activity), shifting population sex and age structure, and by changing prey-selection and reproductive patterns (Robinson *et al.* 2008; Paviolo *et al.*

2009; Ordiz *et al.* 2012; Maletzke *et al.* 2014; Keehner *et al.* 2015). Although legal hunting is intentional and easy to regulate, it can cause declines in carnivore populations, and hunting policies may not align with ecological theory and may suffer from lack of science-based guidelines (Creel *et al.* 2015). Additionally, mismatches between policy and hunting impacts are further complicated by difficulties in accurately measuring trends in population dynamics with standardised monitoring techniques.

European settlers in the Americas viewed predators as a threat, not only to livestock, but also to themselves and to the other wild animals that they relied on for food (Anderson *et al.* 2010). As a result, management of large and medium-sized carnivore populations in the Americas focussed on methods of control or elimination during European colonisation (Gill 2010). Although management varied among and within countries, predators, as a rule, and particularly, wolves (*Canis lupus*), grizzly bears (*Ursus arctos*) and pumas (*Puma concolor*), were managed in three ways to ameliorate the potential threat to livestock (Gill 2010). For the puma, attempted eradication emerged as a strategy based on an agricultural ethic that focussed on eliminating 'undesirable species' as threats to livestock, game animals and people. This strategy dominated until the middle of the 20th century when the sport-hunting strategy emerged, managed by government agencies, to provide recreational opportunity while continuing to address livestock depredation concerns. Finally, a third, more recent strategy of predator protection has emerged, designed to maintain viable puma populations as part of the ecological community (Anderson *et al.* 2010). Although categorised as *Least Concern* on the IUCN Red List because it is a widespread species, the puma is considered to be declining worldwide, including in Argentina, and its conservation presents numerous challenges (Nielsen *et al.* 2016).

In North America, there are numerous studies and substantial information regarding puma demographic parameters and puma management strategies that address conservation, harvest or reduction of livestock depredation (e.g. Logan and Sweaner 2001; Stoner *et al.* 2006; Cooley *et al.* 2009a, 2009b; Anderson *et al.* 2010; Robinson *et al.* 2014; see Table 1). In contrast, puma research in Central and South America is sparse (see Table 1). Currently, in Argentina, puma management is regulated at the province level, and is based on the following three legal strategies: total protection, bounty hunting to reduce population numbers and recreational sport hunting (Walker and Novaro 2010). Yet, there has been little research assessing the effects of these management strategies on puma populations. In fact, most previous puma research in Argentina has been restricted to dietary studies (Donadio *et al.* 2010; Zanón Martínez *et al.* 2012, 2016). Additionally, provincial wildlife departments are underfunded, existing laws are often not enforced because of lack of resources (Walker and Novaro 2010), and under-reporting is likely occurring; thus, we have little information on the status of puma populations that have been exposed to bounty or sport hunting.

In La Pampa province, central Argentina, puma sport hunting was legal until 2007. This region used to attract national and international hunters. From 2002 to 2006, the number of puma trophies in Argentina increased. La Pampa province itself was the principal source of these trophies, where official records

suggested that 40–60 pumas were harvested per year. However, because of under-reporting, the true number of hunted individuals was probably higher, perhaps even in the thousands (Walker and Novaro 2010). In 2007, the Department of Natural Resources of La Pampa province halted puma hunting because of illegal traffic of puma trophies and lack of puma population studies; however, illegal hunting still occurs in this region (J. I. Zanón-Martínez, pers. obs.). Estimating population density is key to informing harvest regulations, creating viable conservation strategies for rare species, monitoring management strategies and evaluating the effects of human actions (Mills 2013). Given the lack of data, there is an urgent need for research that estimates puma density and activity, so as to inform conservation status of puma populations in La Pampa province in areas where they are hunted and not hunted.

Estimating carnivore density, particularly for felines, is difficult; however, camera-trapping methodologies are effective, non-invasive and economical for studying elusive carnivore species such as pumas, which are typically difficult to sample (Kelly *et al.* 2012). The use of camera traps has increased, in part because of advances in quantitative population estimation techniques that can be applied to species where only a portion of the population has natural marks, thereby obtaining better-quality information on highly critical species over large areas of interest (O'Brien 2011). Currently, several studies have expanded on the traditional capture–recapture (CR) models (e.g. Otis *et al.* 1978; Karanth 1995) and used mark–resight (MR; e.g. Arnason *et al.* 1991; White and Shenk 2001; McClintock *et al.* 2009; Rich *et al.* 2014) or spatial mark–resight (SMR) models (e.g. Chandler and Royle 2013; Sollmann *et al.* 2013a, 2013b; Rich *et al.* 2014; Royle *et al.* 2014) to estimate puma densities (Kelly *et al.* 2008; Paviolo *et al.* 2009; Negrões *et al.* 2010; Sollmann *et al.* 2013a; Rich *et al.* 2014).

In the present study, we compared puma densities, prey encounter rates and circadian activity patterns in two areas under different management strategies: a protected area without hunting and a game reserve with sport hunting, within the region of the Caldén forest in La Pampa province. We hypothesised that the densities of puma in our study areas would be a function of prey activity, with higher prey encounter rates resulting in a higher puma density. We also hypothesised that the area with existing human activity (i.e. primarily hunting activity) would have a lower puma density and pumas would change activity patterns from crepuscular or cathemeral to strictly nocturnal.

## Materials and methods

### Study sites

The study area is located in the central region of La Pampa province, Argentina (Fig. 1). This region corresponds to the Caldén District of the Espinal phytogeographic province, which includes habitat types such as Caldén forest, sand grassland and salt deposits (Cabrera 1976). The Caldén forest is situated in central Argentina (between 33.59°S and 40.56°S, and 63.31°W and 65.94°W) and has been severely fragmented by deforestation and conversion to agriculture (González-Roglich *et al.* 2012). The caldenal is a xerophilic forest ecosystem (average canopy tree cover varies from 30% to

Table 1. Puma population densities estimated under different types of management, habitat and methodologies across America

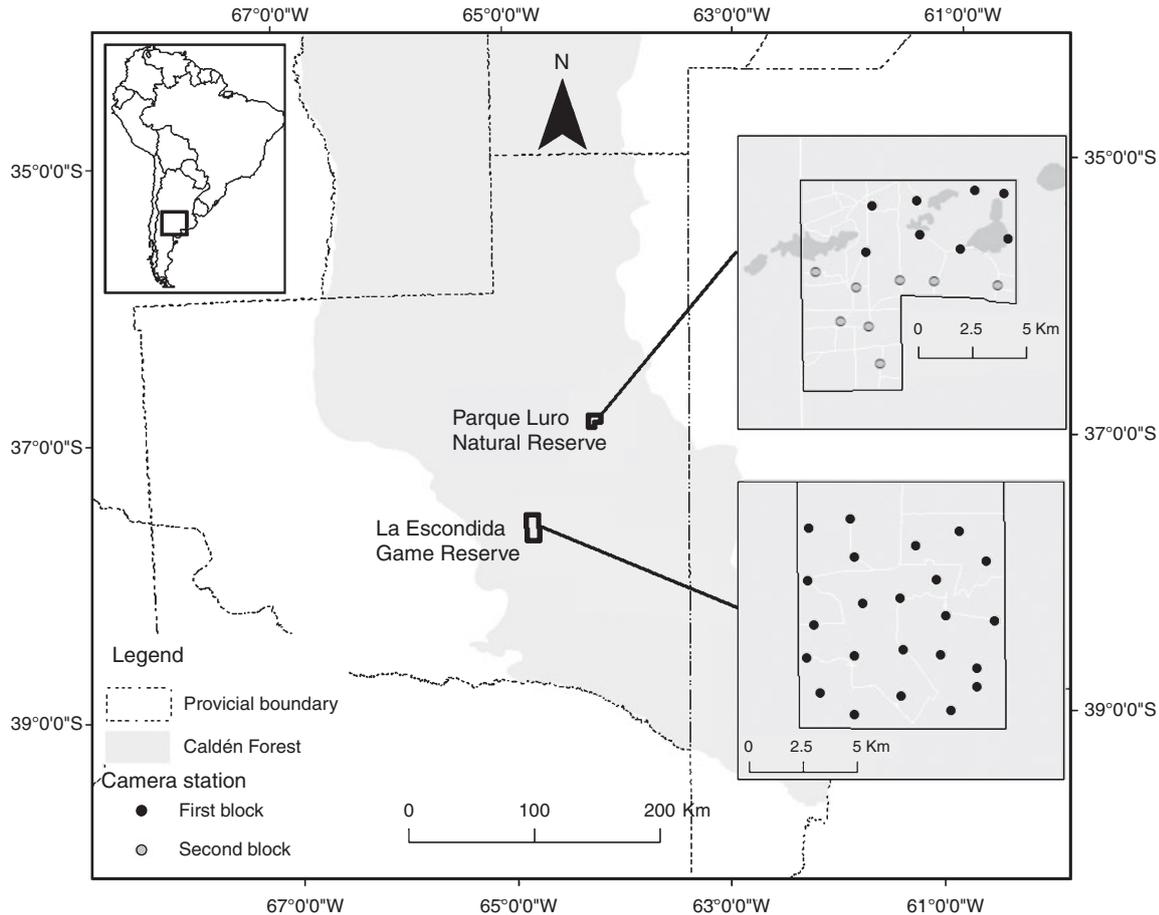
| Site  | Type of habitat  | Protection status of study areas | Abundance  | Survey area (km <sup>2</sup> )       | Adult density (pumas per 100 km <sup>2</sup> ) | Methodology employed              | Reference  |
|---|--|----------------------------------|--|--------------------------------------|--|-----------------------------------|--|
| North America   |  |                                  |  |                                      |  |                                   |  |
| San Andres Mountains, New Mexico, USA                           | San Andres Mountains, desert, scrub                        | Exploited                        | 7.63–14.12   | 703                                  | 1.09–2.01                                      | Telemetry                         | Logan and Sweaner (2001)                                 |
| Wasatch Mountains, Utah, USA                                    | Colorado Plateau and Great Basin Desert                    | Protected<br>Exploited           | 15.24–24.30<br>–   | 1356<br>1300                         | 1.13–1.79<br>3.2                               | Telemetry                         | Stoner <i>et al.</i> (2006)                              |
| Washington, USA   | Cascade, mixed forest                                      | Protected                        | –  | 950                                  | 2.9  | Telemetry                         | Cooley <i>et al.</i> (2009a)                             |
| Colville National Forest, Washington, USA                       | Northern Rocky Mountains, mixed evergreen-deciduous forest | Lightly hunted<br>Heavily hunted | –  | 655                                  | 1.73   | Telemetry                         | Robinson <i>et al.</i> (2008)                            |
| Washington, USA   | Northern Rocky Mountains, mixed evergreen-deciduous forest | Heavily hunted                   | –  | 735                                  | 1.58   | Telemetry                         | Cooley <i>et al.</i> (2009b)                             |
| Collier County, Florida, USA                                    | Forest   | Lightly hunted<br>Protected      | –  | 594<br>1719.13                       | 1.87<br>1.63–1.66                              | Camera-trapping<br>(n = 98)       | Sollmann <i>et al.</i> (2013a)                           |
| Sierra Nanchititla Natural Reserve, Balsas Basin, Mexico        | Forest   | Protected                        | 2–6  | 664                                  | 1.21–6.86                                      | Camera-trapping<br>(n = 10 to 17) | Soria-Diaz <i>et al.</i> (2010)                          |
| Central and South America                                       |  |                                  |  |                                      |  |                                   |  |
| Chiquibul Forest Reserve and National Park, Belize <sup>A</sup> | Subtropical moist forest                                   | Protected                        | 10–14 <sup>B</sup>   | 285–431                              | 2.35–4.91                                      | Camera-trapping<br>(n = 17)       | Kelly <i>et al.</i> (2008) and Rich <i>et al.</i> (2014) |
| Santa Fé Ranch and Cantão State Park, Brazil                    | Tropical forest  | Cattle ranch and protected       | 7.2 <sup>C</sup><br>22 <sup>D</sup>  | 506<br>5002                          | 1.42<br>0.4                                    | Camera-trapping<br>(n = 21)       | Negrões <i>et al.</i> (2010)                             |
| Kaa-Iya del Gran Chaco National Park, Bolivia <sup>A</sup>      | Chaco dry forest   | Protected                        | 9  | 265                                  | 3.4  | Camera-trapping<br>(n = 22)       | Kelly <i>et al.</i> (2008) and Rich <i>et al.</i> (2014) |
| Yaboti' Biosphere Reserve, Argentina <sup>A</sup>               | Humid subtropical forest                                   | Protected                        | 13–18 <sup>B</sup><br>12.9 <sup>C</sup><br>54 <sup>D</sup>                   | 91–105<br>115<br>957                 | 2.4–19.3<br>11.22<br>5.7                       | Camera-trapping<br>(n = 42)       | Kelly <i>et al.</i> (2008) and Rich <i>et al.</i> (2014) |
| Caldenal region, central Argentina <sup>A</sup>                 | Semiarid forest  | Protected                        | 6–8 <sup>B</sup><br>5.9 <sup>C</sup><br>17 <sup>D</sup>                      | 1154–1240<br>986<br>7029             | 0.5–0.81<br>0.6<br>0.2                         | Camera-trapping<br>(n = 16)       | This study   |
|   |  | Exploited                        | 12.76 <sup>C</sup><br>40 <sup>P</sup><br>4.70 <sup>C</sup><br>8 <sup>D</sup> | 136.9<br>817.88<br>248.59<br>1539.97 | 9.32<br>4.89<br>1.98<br>0.52                   | Camera-trapping<br>(n = 23)       |  |

<sup>A</sup>In these studies, three different methodologies were used to estimate puma densities.

<sup>B</sup>Capture–recapture traditional method was used.

<sup>C</sup>Mark–resight was used.

<sup>D</sup>Spatial mark–resight was used. In our study, methodologies 2 and 3 were used.



**Fig. 1.** Locations of study areas, the protected Parque Luro Natural Reserve (76 km<sup>2</sup>) and the hunted La Escondida Game Reserve (200 km<sup>2</sup>) in the Caldén forest in La Pampa province, Argentina, and camera trap-station design within each survey area.

50%, grasslands cover the herbaceous stratum with a low cover of bushes) dominated by Caldén tree (*Prosopis caldenia*). The topography is characterised by plateaux, valleys, hills and plains (ranging from ~50 m to ~200 m, Cano *et al.* 1980). The weather is subhumid-dry, with annual precipitation of 550 mm. The average temperature in summer is 23°C and 8°C in winter, with a minimum of -12°C. The two areas under different management strategies are (1) the 76-km<sup>2</sup> Parque Luro Natural Reserve (PLNR), the only protected area of Caldén forest in La Pampa province, and (2) the 200-km<sup>2</sup> La Escondida Game Reserve (LEGR), a region that has received the highest number of habitat modifications and introductions of ungulates in the past century.

Originally, PLNR was a game reserve. In 1907, red deer (*Cervus elaphus*) and wild boar (*Sus scrofa*) were introduced. In 1968, the area was established as a natural reserve (Amieva 1993) and now PLNR is enclosed by a 2-m-high maintained perimeter fence that prevents deer from exiting the park; however, pumas can get over or under the fence. LEGR was a sheep ranch from 1930 until the mid-1970s, when it was converted to cattle production. In the 1990s, it was established as a game reserve, when management practices began for red deer, wild boar, and, in 1995, blackbuck (*Antelope cervicapra*), which were introduced

for sport hunting. In 2005, the ranch was enclosed with a 2-m-high perimeter fence, preventing deer from exiting the ranch. At present, the game reserve supports multiple human activities such as agriculture, cattle production and game hunting.

#### Camera-trapping surveys

Between June and December 2008, we completed two surveys to estimate abundance of pumas in PLNR and LEGR (Table 2). At each study site, we set camera traps arrayed at regular intervals (2–3 km) in a grid-like formation covering the entire fenced-in area (Fig. 1). The PLNR was subdivided into two sampling blocks of eight camera stations each, and each block was surveyed for 38 consecutive days; thereafter, we moved the camera stations from first block to second block for an additional 38 days, following Design 4 of Nichols and Karanth (2002). In LEGR, we deployed 23 camera stations in a single block, and they were functioning for 90 consecutive days. We placed two unbaited cameras per trapping station on opposing sides of the road or trail, taking advantage of their availability and because pumas often use roads and trails to move. Cameras were active 24 h per day, with a delay of 1 min between triggering events. We visited camera stations every 10 days for routine maintenance. We used Moultrie Game

**Table 2. Summary of puma (*Puma concolor*) camera-trapping grid characteristics in two study areas, the protected Parque Luro Natural Reserve (PLNR) and the hunted La Escondida Game Reserve (LEGR), in La Pampa province, Argentina**

Both reserves are completely fenced and cameras were spaced at 2–3 km apart to cover the entire fenced-in areas

| Study area | Date                    | Area fenced (km <sup>2</sup> ) | Number of camera stations | Survey duration (days) | Survey effort (trap-nights) | %Puma trap success (capture events per 100 trap-nights) |
|------------|-------------------------|--------------------------------|---------------------------|------------------------|-----------------------------|---|
| PLNR       | June–September 2008     | 76                             | 16                        | 76 <sup>A</sup>        | 608                         | 10.69   |
| LEGR       | September–December 2008 | 200                            | 23                        | 90                     | 2070                        | 0.58  |

<sup>A</sup>Eight cameras were moved after 38 days to the second block.

Spy 4.0 MP DGTL white-flash cameras (Moultrie Products, LLC., Alabaster, Alabama, USA). Our sampling period was  $\leq 90$  days to meet the assumption of a closed population (Karanth and Nichols 2002). We defined independent detections of pumas as photo events separated by  $\geq 60$  min (Di Bitetti *et al.* 2006), unless different individuals could be distinguished by subtle marks, or more than one individual was in a single photo.

#### Identification of pumas

Pumas were identified according to protocols in Kelly *et al.* (2008). Three investigators independently identified photographed puma individuals by obvious and subtle markings (e.g. kinked tails, scars, ear nicks, tail-tip coloration and shape, or undercoat spot patterns). Each researcher labelled photographic captures of pumas as either (1) identifiable individuals, (2) marked but not unambiguously identifiable individuals or (3) unmarked individuals following Rich *et al.* (2014).

#### Abundance and densities of pumas by non-spatial mark–resight

We estimated abundance using mark–resight models in Program MARK (McClintock and White 2012). Recently, this technique has been used to estimate puma abundances in Belize, Bolivia and Argentina when only a portion of the population has natural marks (Rich *et al.* 2014). Mark–resight models incorporate photographic captures of uniquely marked (i.e. identifiable individuals), unmarked (i.e. individuals only identifiable to the species level) and marked but not identifiable individuals (McClintock *et al.* 2009; McClintock and White 2012). Encounter histories contain the count of the total number of times an individual was re-sighted during the primary sampling interval and include an overall count of the number of events where pumas were classified as unmarked or as marked but not identifiable (Rich *et al.* 2014). We constructed a three-group, capture–recapture history of individual pumas for each study site by combining identifications made by all investigators, described by Rich *et al.* (2014). The first group corresponded to marked individuals when all investigators agreed on the individual's identification; the second group consisted of individuals marked but unknown, when investigators did not agree on the identification; and the third group consisted of unmarked individuals if more than one investigator identified the photo as unmarked. Our last two categories allowed us to include puma photographs that otherwise would have been discarded in the previous traditional analysis.

In program MARK we used the zero-truncated Poisson-log-normal (zPNE) mark–resight model because marked individuals could not have all-zero encounter histories (i.e. had to be photographed at least once to be known; McClintock *et al.* 2009; McClintock and White 2012; Rich *et al.* 2014). We used the closed resight model because we only had one primary sampling interval. This model included three parameters: the intercept for mean resighting rate ( $\alpha$ ), individual heterogeneity ( $\sigma$ ) and number of unmarked individuals in the population ( $U$ ). We used no covariates and compared two models only: one with no individual heterogeneity (i.e. fixed  $\sigma=0$ ) and one model that estimated  $\sigma$  to test for individual heterogeneity (Rich *et al.* 2014) for each study area. The best models were selected using Akaike's information criterion corrected for a small sample size (AICc), with delta-AIC of  $\leq 2$  denoting competing models (Burnham and Anderson 2002). We used the top-ranked model to derive an estimate of total population size ( $N$ ) and overall mean resighting rate ( $\lambda$ ).

The size of each surveyed area was calculated using a combined capture–recapture history from all investigators to estimate the size of the surveyed area (effective survey area) in both study areas; we used data only from individually identifiable pumas that were detected at two or more camera stations. We calculated the maximum distance moved among camera stations for each unique puma to create an overall mean. Half of this distance (1/2MMDM) was used as the circular buffer radius around each camera-station location (Dice 1938; Wilson and Anderson 1985; Kelly *et al.* 2008; Paviolo *et al.* 2009). We estimated 1/2MMDM and the surveyed areas in ArcView (ESRI 1999) by using X-tools or Spatial Analyst, which we also used to dissolve internal buffers surrounding camera stations and to calculate survey area. We then divided the number of pumas estimated from top model for each survey by the effective survey area, to obtain density of pumas. We estimated standard errors using the delta method described in Nichols and Karanth (2002).

#### Densities of pumas by spatial mark–resight

We used spatial mark–resight (SMR) models that also considered part of the population marked and another part unmarked individuals (Royle *et al.* 2014), which have recently been applied in studies to determine puma (Sollmann *et al.* 2013a; Rich *et al.* 2014) and African lion (*Panthera leo*; Kane *et al.* 2015) densities. Because puma photographic captures were sparse, we grouped data into blocks such that one encounter occasion consisted of 6-day time periods for both study areas, thus avoiding estimated detection rates close to 0 that can prevent model convergence. As with our non-spatial mark–resight methods,

we created capture histories from the uniquely marked individuals and summed detections across encounter occasions. The unmarked pumas constituted those photographs where at least one researcher identified the individual as unmarked. We created capture histories that included an accumulated count of the number of photos of these unmarked pumas at each camera station during each encounter occasion. Marked pumas that we were not able to determine identity for (i.e. marked but unidentifiable) were removed from the analysis, because we would run the risk of underestimating encounter rate and overestimating abundance (Royle *et al.* 2014). We also recorded camera malfunctions, time and location across all encounter occasions.

As in non-spatial mark–resight models, we assumed that marked individuals represent a random subset of population, but, additionally, the marked individuals must represent a random sample of individuals in the State-space  $S$ . We can assume a homogeneous point process for both the marked and the unmarked part of the population. Similar to spatially explicit capture–recapture models, we assumed that each Individual  $i$  has an activity centre,  $s_i$ , and we distributed potential  $s_i$  uniformly across the State-space  $S$ , an area including the trapping grid and a buffer large enough to include all animals potentially exposed to our sampling (Royle *et al.* 2009). We also assumed that the number of Puma  $i$  photographs at Camera station  $j$  and Occasion  $k$ ,  $y_{ijk}$ , was a Poisson random variable with mean encounter rate of  $\lambda_{ijk}$ . We modelled the mean encounter rate using a half-normal decreasing function of the distance from Camera-trap station  $j$  to the individual's Activity centre  $s_i$ , dependent on the baseline trap Encounter rate  $\lambda_0$  (i.e. the probability of capture of Individual  $i$  at Trap  $j$  during a sampling occasion when an individual's Activity centre  $s_i$  is located precisely at Trap  $j$ ) and Parameter  $\sigma$  (i.e. scale parameter of the half-normal function, which relates decline in probability of animal capture with distance away from the activity centre, expressed in kilometres (Royle *et al.* 2009).

To define  $S$ , we used a 10-km buffer in PLNR and a 15-km buffer in LEGR from the outermost coordinates of trapping grids. This resulted in an area for  $S$  of 817.88 km<sup>2</sup> and 1539.97 km<sup>2</sup> in PLNR and LEGR respectively. To ensure that our buffers were large enough to include home-range centers outside the trapping grid, we used the recommended three to four times the estimate of our spatial scalar,  $\sigma$ , to define the state-space (Royle *et al.* 2009). As long as the buffer is sufficiently large,  $S$  will scale with estimated  $N$ , such that density should not change. We implemented the SMR model proposed by Royle *et al.* (2014) using Just Another Gibbs Sampler (JAGS) program through the 'rjags' package interface in software R version 3.0.2 (R Development Core Team 2013). To estimate  $N$ , we applied data augmentation to the marked (50), and unmarked (50) pumas, and  $N$  is the sum of the estimated number of marked individuals and the estimated number of unmarked individuals (Royle *et al.* 2014). For the unmarked pumas, encounter histories are latent (i.e. unobservable) and we observed only the accumulated counts of unmarked pumas, and, thus, these are essentially considered as missing data (Sollmann *et al.* 2013b). We adapted a Bayesian framework and used Markov-chain Monte Carlo (MCMC) sampling to update missing data using their full conditional distribution (Sollmann *et al.* 2013a; Rich *et al.* 2014; Royle *et al.* 2014). For each study area, we ran three chains of the MCMC

sampler with 200 000 iterations each, discarding 100 000 iterations as burn-in. We calculated the Gelman–Rubin statistic  $R$ -hat (Gelman *et al.* 2004) using the R package coda to check for chain convergence (Plummer *et al.* 2006); values <1.1 indicated chain convergence. We reported the posterior mean with standard error (defined as the standard deviation of the posterior distribution of a parameter) and the Bayesian credible intervals. For density estimates we reported the mode rather than the mean because simulations have shown the mode to be less biased than the mean with low sample sizes (Chandler and Royle 2013; Sollmann *et al.* 2013b; Rich *et al.* 2014). Density,  $D$ , was derived by dividing  $N$  by the area of  $S$ .

#### *Comparing density estimates of puma between study areas and techniques*

We compared puma densities between studies areas, PLNR and LEGR, and between modelling techniques MR and SMR. We considered estimates to be different from each other if their 95% confidence or credible intervals did not overlap each other (Payton *et al.* 2003).

#### *Encounter rate of prey*

We calculated and compared encounter rates for prey species between the two study areas to explore relationships with puma densities. For each prey species, we recorded the photographic rate (number of photographic events of prey species/100 trap-days). A photographic event consisted of photo captures of any distinctly different individuals of a species within a 60-min time period, regardless of number of photographs. We grouped prey into the following different categories: large mammals (red deer, wild boar, blackbuck and guanaco (*Lama guanicoe*)); medium mammals (European hare (*Lepus europaeus*), Patagonian mara (*Dolichotis patagonum*), large hairy armadillo (*Chaetophractus villosus*) and plains viscacha (*Lagostomus maximus*)); big birds (lesser rhea (*Rhea americana*)); medium birds (tinamidae (*Nothoprocta cinerascens*), *Eudromia elegans* and *Nothura* sp.) and small birds (eared dove (*Zenaida auriculata*)). We considered prey encounter rates to be different between study areas if 95% confidence intervals (CIs) did not overlap (Payton *et al.* 2003).

#### *Activity patterns*

We used the time printed on photographs obtained during the surveys to describe puma activity patterns. To avoid autocorrelation, we considered records to be independent if they were more than 1 h apart at the same station, except when it was possible to identify distinct puma individuals (Silveira *et al.* 2003; Ridout and Linkie 2009). Because puma behaviour might be conditioned on the events of sunrise and sunset, we first recalculated the time records as time to (or from) those astronomical events (Nouvellet *et al.* 2012) and then standardised them to a 24-h day to allow comparison between different surveys and seasons. We compared puma activity patterns between PLNR and LEGR using Mardia–Watson–Wheeler test to assess whether the daily frequency distributions of captures of two different samples have the same distribution (Batschelet 1981; Paviolo *et al.* 2009).

Also, we classified puma activity patterns into the following four categories according to van Schaik and Griffiths (1996): (1) diurnal, when puma’s activity is between 1 h after the sunrise and 1 h before the sunset; (2) nocturnal, when puma’s activity is between 1 h after the sunset and 1 h before the sunrise; (3) cathemeral, when puma’s activity is distributed approximately evenly throughout the 24 h of the daily cycle, or when significant amounts of activity occur within both the light and dark portions of that cycle; and (4) crepuscular, when puma’s activity occurred 1 h before and after sunrise and sunset. Then, we fit kernel-density functions to time of observations of pumas to describe activity patterns and calculate the temporal overlap in puma activity between the two sites with the  $\Delta_1$  overlap term (Ridout and Linkie 2009). The  $\Delta_1$  overlap term is suggested for small samples of a quantitative index  $\Delta$  of overlap, which ranges from 0 to 1 and is calculated as the area under the curve formed by taking the smaller of two density functions at each time point (Ridout and Linkie 2009). Thus, values close to 1 amount to large temporal overlap in puma activity at PLNR versus LEGR. Finally, we obtained 95% CIs for these estimates from 10 000 bootstrap samples. All statistics were analysed using the overlap package (Ridout and Linkie 2009) in the software R 3.0.2 (R Development Core Team 2013).

**Results**

*Camera-trapping surveys and identification of pumas*

We accumulated 608 trap-nights in 76 days in PLNR and 2070 trap-nights in 90 days at LEGR (Table 2). We obtained 65 and 12 puma photographs as independent events, corresponding to 10.69 and 0.58 capture events per 100 trap-nights in PLNR and LEGR respectively (Table 2). Interestingly, most puma photographs were identified to the individual level, namely, 61 of 65 events in PLNR and 10 of 12 events in LEGR. Pumas categorised as marked but not identifiable were 0 and 1, and those categorised as unmarked were 4 and 1 in PLNR and LEGR respectively (Table 3).

*Abundance and densities of pumas by non-spatial mark–resight*

For PLNR, the mark–resight model without individual heterogeneity had the most support. Conversely, the best model for LEGR included individual heterogeneity. Top-ranking models resulted in abundance estimates that were higher in PLNR (mean  $\pm$  s.e.;  $12.76 \pm 0.37$ ) than in LEGR ( $4.70 \pm 0.56$ ; Table 3).

At PLNR, the 1/2MMDM value was 2.75 km and the area surveyed was 136.87 km<sup>2</sup> and in LEGR the 1/2MMDM was 4.03 km and the area surveyed was 248.59 km<sup>2</sup> (Table 3). Puma density ( $D \pm$  s.e.) was considerably higher at PLNR at  $9.32 \pm 1.05$  pumas per 100 km<sup>2</sup>, than at LEGR with  $1.98 \pm 0.27$  pumas per 100 km<sup>2</sup> (Table 3).

*Densities of pumas by spatial mark–resight*

The posterior mean density using Bayesian techniques ( $D \pm$  s.e.) was also higher at PLNR at  $4.90 \pm 1.51$  than at LEGR at  $1.38 \pm 0.91$  pumas per 100 km<sup>2</sup>; for both study areas, the posterior mode was lower, at 4.89 (slightly) and 0.52 pumas per 100 km<sup>2</sup>, respectively. The baseline encounter rate,  $\lambda_0$ , was higher in PLNR ( $0.24 \pm 0.08$ ) than in LEGR ( $0.02 \pm 0.03$ ) and the posterior mean for the movement parameter  $\sigma$  was smaller in PLNR ( $3.25 \pm 0.77$ ) than in LEGR ( $6.00 \pm 1.78$ ) (Table 4). All parallel Markov chains appeared to converge, as the Gelman–Rubin statistic R-hat for all parameters was <1.1

*Comparing density estimates of puma between study areas and techniques*

Regardless of the modelling technique used, densities of pumas were always higher in PLNR than LEGR, as indicated by non-overlapping CIs. Spatial mark–resight (SMR) models were more conservative, generally producing lower puma estimates than those from non-spatial mark–resight techniques (Fig. 2a).

**Table 3. Number of pumas (*Puma concolor*) recorded and comparisons of models with and without heterogeneity used to estimate puma abundance in the protected Parque Luro Natural Reserve and the hunted La Escondida Game Reserve from La Pampa province, Argentina**

Puma classifications were made in conjunction with three investigators. Half mean of the maximum distances moved (1/2MMDM) among individuals was used as a radius around camera traps to determine the effective survey areas. Density was estimated from the abundance estimate ( $N$ ) from the top model for Parque Luro Natural Reserve.  $\alpha$ , mean resight rate;  $\sigma$ , individual heterogeneity;  $U$ , number of unmarked individuals;  $(.)$ , parameter constant;  $(0)$ , parameter set to 0;  $\lambda$ , the overall mean resighting rate;  $n^*$ , the number of pumas identified to the individual level;  $II$ , the total number of puma photographic-capture events classified as individually identifiable;  $MBNI$ , the number of pumas marked but not unambiguously identifiable; and  $UM$ , unmarked pumas;  $AICc$ , Akaike’s information criterion with small sample size;  $\Delta AICc$ , differences in  $AICc$ ;  $\text{Log}(l)$ , maximized log likelihood;  $K$ , number of estimable parameters;  $\omega_i$ , Akaike weights

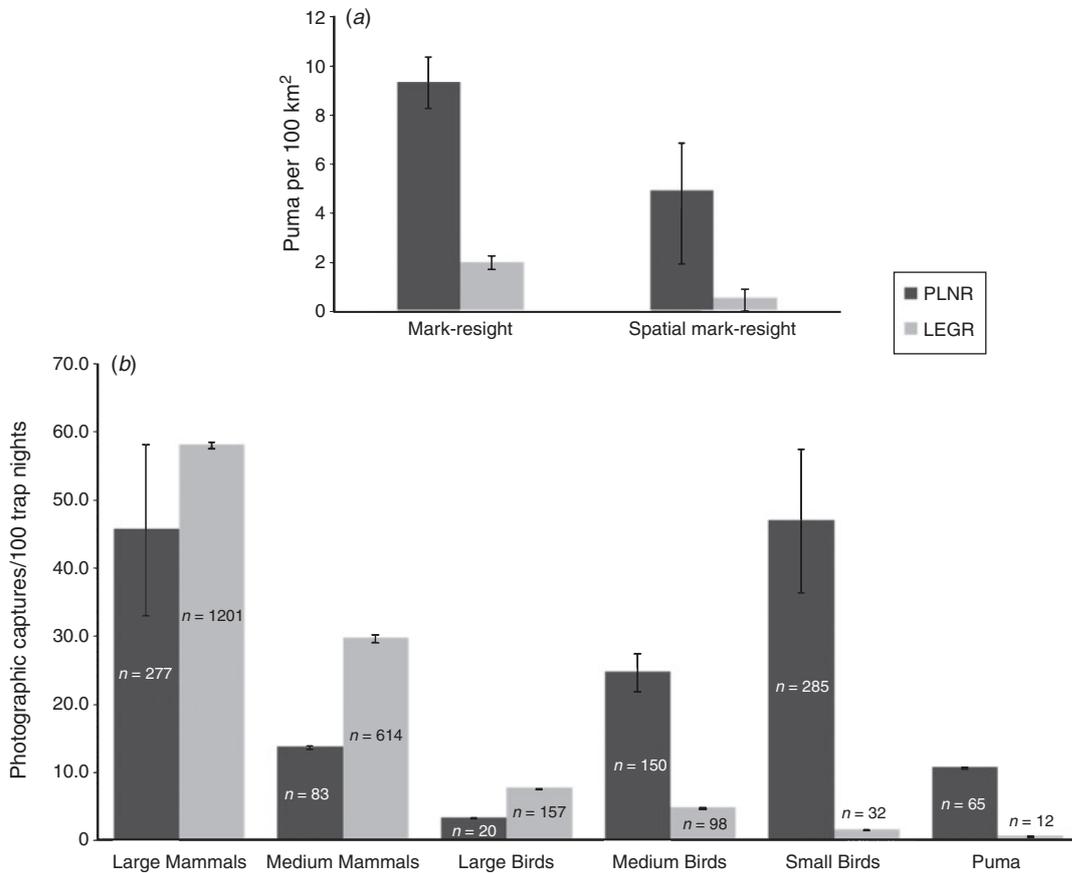
| Site                        | Number of puma photographic-capture events |    |      |    | Model definition <sup>a</sup> | AICc  | $\Delta AICc$ | Log( $l$ ) | $K$ | $\omega_i$ | $N$ (s.e.)   | $\lambda$ (s.e.) | 1/2 MMDM (km) | Effective survey area (km <sup>2</sup> ) | Density (s.e.) per 100 km <sup>2</sup> |
|-----------------------------|--|----|------|----|-------------------------------|-------|---------------|------------|-----|------------|--------------|------------------|---------------|--|--|
|                             | $n^*$                                      | II | MBNI | UM |                               |       |               |            |     |            |              |                  |               |  |  |
| Parque Luro Natural Reserve | 12   | 61 | 0    | 4  | $\alpha(.)\sigma(0)U(.)$      | 62.61 | 0.00          | 57.41      | 2   | 0.83       | 12.76 (0.37) | 5.05 (0.66)      | 2.75          | 136.87                                   | 9.32 (1.05)                            |
|                             |  |    |      |    | $\alpha(.)\sigma(.)U(.)$      | 65.80 | 3.20          | 57.14      | 3   | 0.17       | 12.74 (0.40) | 5.03 (0.72)      |               |  |  |
| La Escondida Game Reserve   | 4  | 10 | 1    | 1  | $\alpha(.)\sigma(.)U(.)^A$    | 23.30 | 0.00          | 13.30      | 3   | 0.50       | 4.70 (0.56)  | 2.45 (0.85)      | 4.03          | 248.59                                   | 1.98 (0.27)                            |

<sup>A</sup>Because of the small sample size, the models with and without individual heterogeneity could not be distinguished; therefore, we used the heterogeneity model as there was support for this model in the traditional modelling approach (i.e. Program CAPTURE not included in the this paper).

**Table 4.** Summary statistics of parameter estimates from a spatial mark–resight model incorporating photographic captures of puma (*Puma concolor*) from camera-trapping surveys conducted in the protected Parque Luro Natural Reserve and the hunted La Escondida Game Reserve

All model parameters converged as the Gelman–Rubin R-hat of <1

| Parameter                                  | Parque Luro Natural Reserve |      |       |        | La Escondida Game Ranch |      |       |        |
|--|-----------------------------|------|-------|--------|-------------------------|------|-------|--------|
|  | Mean (s.e.)                 | Mode | 2.50% | 97.50% | Mean (s.e.)             | Mode | 2.50% | 97.50% |
| $\sigma$ (km)                              | 3.25 (0.77)                 | 2.89 | 2.35  | 5.40   | 6.00 (1.78)             | 4.70 | 3.18  | 9.63   |
| $\lambda_0$ (daily mean encounter rate)    | 0.24 (0.08)                 | 0.20 | 0.14  | 0.42   | 0.02 (0.03)             | 0.01 | 0.01  | 0.08   |
| $N$ (super population)                     | 40.08 (12.35)               | 40   | 16    | 64     | 21.33 (14.07)           | 8    | 6     | 57     |
| $D$ (individuals per 100 km <sup>2</sup> ) | 4.90 (1.51)                 | 4.89 | 1.96  | 7.83   | 1.38 (0.91)             | 0.52 | 0.39  | 3.70   |



**Fig. 2.** Estimated densities and encounter rates in the protected Parque Luro Natural Reserve (PLNR) and the hunted La Escondida Game Reserve (LEGR). (a) Puma (*Puma concolor*) density, and the associated 95% confidence intervals, calculated by the following two methods: mark–resight with 95% confidence intervals, and spatial mark–resight (with 95% credible intervals) models from camera-trapping surveys. (b) Potential prey and puma encounter rates (number of photographic-capture events per 100 trap-nights) from camera-trap surveys; error bars are 95% confidence intervals;  $n$ , total number of photographic events.

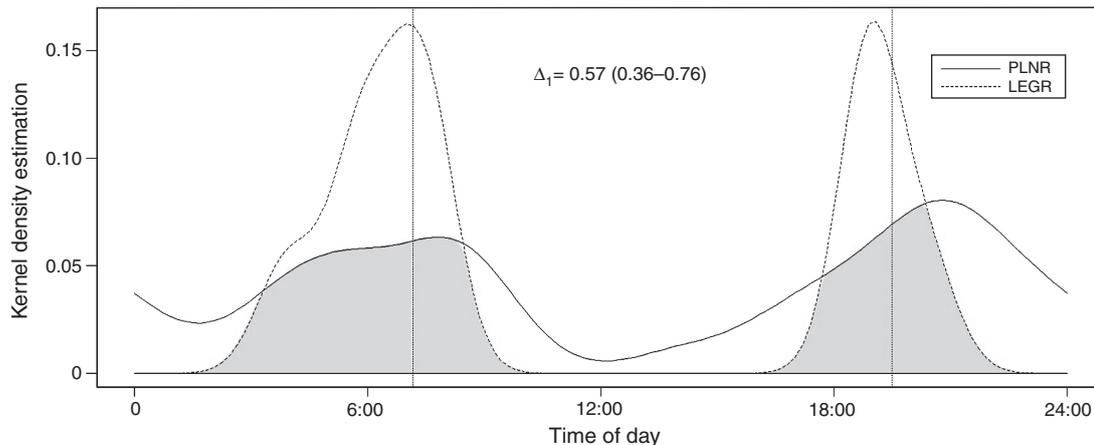
*Prey encounter rates*

Prey encounter rates varied within and between study sites (Fig. 2b). Interestingly, the protected PLNR had a lower prey species richness than did the hunted LEGR, because blackbuck, guanaco, Patagonian mara and plains viscacha were not present. However, the large-mammal potential-prey category showed similar encounter rates across sites (i.e. overlapping 95% CIs; Fig. 2b), although there was much higher variability at PLNR. Medium-sized mammals and large birds had higher

encounter rates in the hunted LEGR than in the protected PLNR, whereas medium-bird, small-bird and puma encounter rates were higher in PLNR than LEGR (Fig. 2b).

*Activity patterns*

Daily puma activity patterns were not different between PLNR and LEGR (Mardia–Watson–Wheeler test,  $\chi^2 = 1.26$ , d.f. = 2,  $P = 0.53$ ). However, puma activity was spread more evenly around the clock at the protected PLNR, although being



**Fig. 3.** Puma (*Puma concolor*) activity patterns based on kernel-density estimation on circular data from camera-trapping records from the protected Parque Luro Natural Reserve (PLNR,  $n = 65$  photo events, black line) and the hunted La Escondida Game Reserve (LEGR,  $n = 12$ , photo events, dashed line). Temporal activity overlap in puma activity between PLNR and LEGR is represented by  $\Delta_1$ , which ranges from 0 (no temporal overlap) to 1 (complete temporal overlap) and is calculated as the area under the curve formed (shaded grey). The black dashed lines represent times of sunrise and sunset.

predominately nocturnal (0.50 of kernel density), with a minor peak at just before 0600 hours and a larger peak at ~2200 hours. At the hunted LEGR, puma activity peaked dramatically just before 0700 hours and again at 1900 hours (Fig. 3) and pumas exhibited no activity from ~1000 hours to 1700 hours, although most activity was also nocturnal (0.41 of kernel density). The density functions showed that pumas in both study areas had some crepuscular activity, both at sunrise and sunset, but in PLNR pumas could be active during any time of the day (Fig. 3). Despite no significant difference, overall puma activity patterns appeared different between the study areas, with a low level of overlap,  $\Delta_1 = 0.57$ , between the sites (Fig. 3).

## Discussion

Regardless of the estimation method, density of pumas was always higher in the protected PLNR (range = 4.89–9.32 pumas per 100 km<sup>2</sup>) than in the LEGR (range = 0.52–1.98 pumas per 100 km<sup>2</sup>) study site. Additionally, our results showed that the densities of pumas were not a function of prey trapping rate and activity patterns of pumas were different between PLNR and LEGR, which could have been influenced by existence of human activity.

Our density estimates in PLNR were also substantially higher than were density estimates reported in other protected areas from Argentina (range 0.3–1.55 pumas km<sup>-2</sup>) (Kelly *et al.* 2008; Paviolo *et al.* 2009; Quiroga *et al.* 2016). The protected PLNR is a forest island surrounded by agriculture and cattle ranches, and pumas are likely to use the forest for refuge, because this reserve includes high-quality habitat. Pumas are hunted and captured in the ranches neighbouring PLNR, where we obtained photographs of an adult male with a snare cable around its abdomen. Additionally, forest rangers have noted pumas with leg snares several times. Woodroffe and Ginsberg (1998) considered border areas of reserves as high risk for predators because of the conflict with people on reserve borders that can be a major cause of carnivore mortality. Thus, PLNR could act as a source patch

within the landscape, yet the border edges could be a sink, owing to a high levels of emigration of young individuals that may suffer high mortality as they disperse from PLNR. Protected areas, such as national parks or lightly hunted areas, are generally source areas for pumas (Laundré and Clark 2003), which have been shown to exhibit higher densities than in areas with higher hunting intensity (Stoner *et al.* 2006; Cooley *et al.* 2009a, 2009a; Robinson *et al.* 2014). Also, in this ecosystem, forest refugia in the Caldén forest such as PLNR, lack jaguars (*Panthera onca*), which could potentially contribute to higher puma densities in the area, because pumas may be freed from intraspecific competition for prey resources or from direct killing by jaguars, and thus may increase in abundance or expand their spatio-temporal niches (Palomares and Caro 1999).

From 2000 to 2007, puma hunting was permitted in LEGR, and, in 2007, three individuals, namely two females and one male, were harvested (L. Córdoba, pers. comm., LEGR manager). Total numbers of pumas hunted in other years are unknown. However, the low puma density in LEGR is similar to the density estimated in the Atlantic Forest of Argentina ( $0.67 \pm 0.16$  pumas per 100 km<sup>2</sup>), where poaching and illegal timber extraction have a negative impact on the population density of pumas (Kelly *et al.* 2008; Paviolo *et al.* 2009). LEGR could act as an ecological trap for pumas, because LEGR appears to have high diversity and high encounter rates of prey. Several North American studies have shown that heavily hunted areas act as sinks, where puma densities can be similar to those in source areas as a result of the immigration of individuals into hunted (sink) populations (Stoner *et al.* 2006; Robinson *et al.* 2008; Cooley *et al.* 2009a, 2009b).

Another cause of decline of large wild-cat populations is low prey abundance (Sunquist and Sunquist 2002; Wilson and Mittermeier 2009), and, in general, puma abundance depends largely on prey abundance (Pierce 2000; Logan and Sweanor 2001). Paviolo *et al.* (2009) suggested that low abundance of pumas in the Green Corridor of north-eastern Argentina could be attributed to low abundance of prey. Our trapping rates of

potential prey (i.e. large mammals) were similar and high in both study areas; however, in the protected PLNR, high encounter rates of introduced ungulates, namely red deer and wild boar, corresponded with a high density of pumas, perhaps indicating a numerical response of predators to prey. However, this was not the case in the hunted LEGR, where puma density was low despite high large-prey encounter rates. Red deer are restricted to PLNR, because of the high perimeter fence, yet the fencing does not work for wild boar. Additionally, there are no other native herbivores such as guanacos and pampas deer (*Ozotoceros bezoarticus*) that could compete for food resources. Thus, large introduced herbivores in the PLNR could be closer to ecological carrying capacity and, therefore, availability of this species may be high, as is evident in PLNR puma-diet analyses (Zanón Martínez *et al.* 2016).

The behaviour of wildlife can be influenced by anthropogenic activity. Pumas were recorded during all hours in the protected PLNR, whereas in the hunted LEGR, pumas were rarely active during the middle of the day (1000 hours to 1600 hours; albeit we note that sample sizes were small for LEGR). Higher nocturnal puma behaviour exhibited at LEGR could be due to higher human activity and hunting of pumas during daylight hours. This effect has been shown in other studies where pumas were more active during the first hours of the day in the well protected area, whereas in the least-protected areas they showed bimodal activity peaks, being active in the early morning and early evening, and remaining active during the night (Paviolo *et al.* 2009). Our study showed even stronger evidence of bimodal activity (at 0700 hours and 1900 hours) at the site with high human disturbance.

Determining demographic parameters such as population density for a large carnivore is crucial to understanding the impacts of past management practices and is necessary to outline future conservation and management plans (Gittleman *et al.* 2001; Ray *et al.* 2005; Mills 2013). We used camera-trap information on puma populations where a majority of the population was individually identifiable by obvious and subtle marks and we used a mark–resight and a spatial mark–resight modelling framework to incorporate unmarked animal photo captures into our estimates of abundance and density. Traditional capture–recapture models have been applied to estimate abundance in puma populations (Kelly *et al.* 2008; Paviolo *et al.* 2009; Negrões *et al.* 2010); however, in these studies, ambiguous photos were discarded and thus not used in the analyses, removing valuable information on puma captures. Mark–resight models incorporate information from both marked and unmarked individuals, to obtain a more reliable population-size estimate (Sollmann *et al.* 2013a; Rich *et al.* 2014; Royle *et al.* 2014). Spatial mark–resight models (SMR) also take the camera locations directly into the estimation process and, thus, avoid problems associated with using *ad hoc* methods to convert abundance to density (Efford 2004; Borchers and Efford 2008; Royle *et al.* 2009, 2014).

Densities of pumas estimated from SMR models were more conservative than those estimated from traditional capture–recapture and mark–resight techniques. Similar results have been reported by Rich *et al.* (2014), suggesting that non-spatial models are likely to not fully account for animal movement out of the sampling grid, such that 1/2MMDM may

be too small to accurately reflect animal movements, potentially leading to overestimation of density, which is highly problematic for species conservation. When we applied the SMR models, we defined the spatial extent of the puma populations in both study areas by setting a state-space,  $S$ , to be large enough to include all animals potentially exposed to our sampling (Royle *et al.* 2009), including pumas occurring outside the fences and the camera grid. Thus, the spatial models were not confined to the minimum convex polygon (MCP) of the camera grids themselves. However, we do recognise that the sizes of our study areas were small and the number of camera stations fewer than in other studies that have estimated puma density (Kelly *et al.* 2008; Paviolo *et al.* 2009; Negrões *et al.* 2010). We also note that our study was unreplicated and, thus, should be interpreted with caution. Given that small fenced reserves established for sport hunting are common in La Pampa province, we urge future studies to focus on such reserves to provide much needed information on the status of puma populations in such areas.

### *Conservation of pumas in La Pampa*

We have provided the first density estimates of pumas for a semi-arid forest in South America, including two areas under different management scenarios, i.e. with and without sport hunting of both pumas and their prey. In Argentina, mainly in La Pampa province, hunting pumas for sport or predator control is legal. Sport hunting is not well regulated; in fact, hunting permits are granted without reliable information on population status of this species. For example, puma hunting is permitted in game reserves as small as 10 km<sup>2</sup>.

Our findings of lower puma density in a hunted game reserve despite high prey encounter rates, is useful information for wildlife managers in La Pampa province, and points to the need for future study on the long-term viability of the puma in such reserves. Additionally, we demonstrated that the protected and intact forest, although small, at PLNR can hold high puma densities. There are 56 similar fenced-in game reserves located in the Caldenal region covering over 3222 km<sup>2</sup> or 4.4% of the ecosystem in the province (González-Roglich *et al.* 2012). Most have high abundance of large prey species and optimal habitat, and, therefore, may have high puma densities too. Pumas may be drawn into the areas by potential large prey as fences do not deter pumas. However, in this province, threats to puma populations are still present, mainly through poaching. In La Pampa province, the puma is not endangered; however, if sport hunting is to be a viable strategy, it is necessary to develop and implement management plans for puma populations, together with strict control over game reserves. The hunting of pumas in La Pampa province requires an adequate regulatory scheme to assure the viability of this species. For hunting to be viable, it is likely that some reserves will need to be strictly protected, such as PLNR, so as to act as safe refuges for pumas across the landscape.

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## References

- Amieva, E. O. (1993). 'El Parque Luro'. (Fondo Editorial Pampeano: Santa Rosa, Argentina.)
- Anderson, C. R., Lindzey, F., Knopff, K. H., Jalkotzy, M. G., and Boyce, M. S. (2010). Cougar management in North America. In 'Cougar: Ecology and Conservation'. (Eds M. Hornocker and S. Negri.) pp. 41–54. (The University of Chicago Press: Chicago, IL.)
- Arnason, A. N., Schwarz, C. J., and Gerrard, J. M. (1991). Estimating closed population size and number of marked animals from sighting data. *The Journal of Wildlife Management* **55**, 716–730. doi:10.2307/3809524
- Batschelet, E. (1981). 'Circular Statistics in Biology.' (Academic Press: New York.)
- Borchers, D. L., and Efford, M. G. (2008). Spatially explicit maximum likelihood methods for capture-recapture studies. *Biometrics* **64**, 377–385. doi:10.1111/j.1541-0420.2007.00927.x
- Burnham, K. P., and Anderson, D. (2002). 'Model Selection and Multi-model Inference: a Practical Information-theoretic Approach.' 2nd edn. (Springer: New York.)
- Cabrera, A. L. (1976). 'Regiones Fitogeográficas Argentinas.' (ACME: Buenos Aires.)
- Cano, E., Fernández, B., and Montes, D. M. (1980). 'Inventario Integrado de los Recursos Naturales de la Provincia de La Pampa.' (UNLPam, Gobierno de La Pampa e INTA: Buenos Aires.)
- Chandler, R. B., and Royle, J. A. (2013). Spatially-explicit models for inference about density in unmarked populations. *The Annals of Applied Statistics* **7**, 936–954. doi:10.1214/12-AOAS610
- Cooley, H. S., Wielgus, R. B., Koehler, G. M., Robinson, H. S., and Maletzke, B. T. (2009a). Does hunting regulate cougar populations? A test of the compensatory mortality hypothesis. *Ecology* **90**, 2913–2921. doi:10.1890/08-1805.1
- Cooley, H. S., Wielgus, R. B., Koehler, G., and Maletzke, B. (2009b). Source populations in carnivore management: cougar demography and emigration in a lightly hunted population. *Animal Conservation* **12**, 321–328. doi:10.1111/j.1469-1795.2009.00256.x
- Creel, S., Becker, M., Christianson, D., Dröge, E., Hammerschlag, N., Hayward, M. W., Karanth, U., Loveridge, A., Macdonald, D. W., Matandiko, W., M'soka, J., Murray, D., Rosenblatt, E., and Schuette, P. (2015). Questionable policy for large carnivore hunting. *Science* **350**, 1473–1475. doi:10.1126/science.aac4768
- Di Bitetti, M. S., Paviolo, A., and 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.
- Dice, L. R. (1938). Some census methods for mammals. *The Journal of Wildlife Management* **2**, 119–180. doi:10.2307/3796432
- Donadio, E., Novaro, A. J., Buskirk, S. W., Wursten, A., Vitali, M. S., and Monteverde, M. J. (2010). Evaluating a potentially strong trophic interaction: pumas and wild camelids in protected areas of Argentina. *Journal of Zoology* **280**, 33–40. doi:10.1111/j.1469-7998.2009.00638.x
- Efford, M. (2004). Density estimation in live-trapping studies. *Oikos* **106**, 598–610. doi:10.1111/j.0030-1299.2004.13043.x
- ESRI (1999). Getting to Know ArcView GIS: the Geographic Information System (GIS) for Everyone. Environmental Systems Research Institute, Inc., Redlands, CA
- Gelman, A., Carlin, J. B., Stern, H. S., and Rubin, D. B. (2004). 'Bayesian Data Analysis.' 2nd edn. (CRC/Chapman & Hall: Boca Raton, FL.)
- Gill, R. B. (2010). To save a mountain lion: evolving philosophy of nature and cougars. In 'Cougar: Ecology and Conservation'. (Eds M. Hornocker and S. Negri.) pp. 5–16. (University of Chicago Press: Chicago, IL.)
- Gittleman, J. L., MacDonald, D. W., Wayne, R. K., and Gosling, M. (2001). 'Carnivore Conservation.' (Cambridge University Press: Cambridge, UK.)
- González-Roglich, M., Southworth, J., and Branch, L. C. (2012). The role of private lands for conservation: land cover change analysis in the Caldenal savanna ecosystem, Argentina. *Applied Geography (Sevenoaks, England)* **34**, 281–288. doi:10.1016/j.apgeog.2011.12.002
- Kane, M. D., Morin, D. J., and Kelly, M. J. (2015). Potential for camera-traps and spatial mark-resight models to improve monitoring of the critically endangered West African lion (*Panthera leo*). *Biodiversity and Conservation* **24**, 3527–3541. doi:10.1007/s10531-015-1012-7
- Karanth, K. U. (1995). Estimating tiger *Panthera tigris* populations from camera-trap data using capture-recapture models. *Biological Conservation* **71**, 333–338. doi:10.1016/0006-3207(94)00057-W
- Karanth, K. U., and Nichols, J. (2002). 'Monitoring Tigers and their Prey: a Manual for Researchers, Managers and Conservationists in Tropical Asia.' (Center for Wildlife Studies: Bangalore, India.)
- Keehner, J. R., Wielgus, R. B., Maletzke, B. T., and Swanson, M. E. (2015). Effects of male targeted harvest regime on sexual segregation in mountain lion. *Biological Conservation* **192**, 42–47. doi:10.1016/j.biocon.2015.09.005
- Kelly, M. J., Betsch, J., Wulsch, C., Mesa, B., and Mills, S. L. (2012). Noninvasive sampling for carnivores. In 'Carnivore Ecology and Conservation: a Handbook of Techniques'. (Eds L. Boitani and R. A. Powell.) pp. 47–69. (Oxford University Press: New York.)
- Kelly, M. J., Noss, A. J., Di Bitetti, M. S., Maffei, L., Arispe, R. L., Paviolo, A., De Angelo, C., and Di Blanco, Y. (2008). Estimating puma densities from camera trapping across three study sites: Bolivia, Argentina, and Belize. *Journal of Mammalogy* **89**, 408–418. doi:10.1644/06-MAMM-A-424R.1
- Laundré, J., and Clark, T. W. (2003). Managing puma hunting in the western United States: through a metapopulation approach. *Animal Conservation* **6**, 159–170. doi:10.1017/S1367943003003202
- Logan, K., and Sweanor, L. L. (2001). 'Desert Puma: Evolutionary Ecology and Conservation of an Enduring Carnivore.' (Island Press: Washington, DC.)
- Maletzke, B. T., Wielgus, R., Koehler, G. M., Swanson, M., Cooley, H., and Allredge, J. R. (2014). Effects of hunting on cougar spatial organization. *Ecology and Evolution* **4**, 2178–2185.
- McClintock, B. T., and White, G. C. (2012). From NOREMARK to MARK: software for estimating demographic parameters using mark-resight methodology. *Journal für Ornithologie* **152**, 641–650. doi:10.1007/s10336-010-0524-x
- McClintock, B. T., White, G. C., Antolin, M. F., and Tripp, D. W. (2009). Estimating abundance using mark-resight when sampling is with replacement or the number of marked individuals is unknown. *Biometrics* **65**, 237–246. doi:10.1111/j.1541-0420.2008.01047.x
- Mills, S. L. (2013). 'Conservation of Wildlife Populations: Demography, Genetics, and Management.' 2nd edn. (Wiley-Blackwell: Hoboken, NJ.)
- Negrões, N., Sarmento, P., Cruz, J., Eira, C., Revilla, E., Fonseca, C., Sollmann, R., Torres, N. M., Furtado, M. M., Jacomo, A. T. A., and Silveira, L. (2010). Use of camera-trapping to estimate puma density and influencing factors in central Brazil. *The Journal of Wildlife Management* **74**, 1195–1203. doi:10.2193/2009-256

- Nichols, J. D., and Karanth, K. U. (2002). Statistical concepts: estimating absolute densities of tigers using capture-recapture sampling. In 'Monitoring Tigers and their Prey: a Manual for Researchers, Managers and Conservationists in Tropical Asia'. (Eds K. U. Karanth and J. D. Nichols.) pp. 121–137. (Center for Wildlife Studies: Bangalore, India.)
- Nielsen, C., Thompson, D., Kelly, M., and Lopez-Gonzalez, C. A. (2016). *Puma concolor*. In 'The IUCN Red List of Threatened Species 2016'. e.T18868A97216466. Available at <http://www.iucnredlist.org/details/18868/0>. [Verified 28 July 2016]
- Nouvellet, P., Rasmussen, G. S. A., MacDonald, D. W., and Courchamp, F. (2012). Noisy clocks and silent sunrises: measurement methods of daily activity pattern. *Journal of Zoology* **286**, 179–184. doi:10.1111/j.1469-7998.2011.00864.x
- O'Brien, T. G. (2011). Abundance, density and relative abundance: a conceptual framework. In 'Camera Traps in Animal Ecology'. (Eds A. F. O'Connell, J. D. Nichols and K. U. Karanth.) pp. 71–96. (Springer: New York.)
- Ordiz, A., Støen, O.-G., Sæbø, S., Kindberg, J., Delibes, M., and Swenson, J. E. (2012). Do bears know they are being hunted? *Biological Conservation* **152**, 21–28. doi:10.1016/j.biocon.2012.04.006
- Otis, D. L., Burnham, K., White, G. C., and Anderson, D. (1978). Statistical inference from capture data on closed animal populations. *Wildlife Monographs* **62**, 1–135.
- Palomares, F., and Caro, T. M. (1999). Interspecific killing among mammalian carnivores. *American Naturalist* **153**, 492–508. doi:10.1086/303189
- Paviolo, A., Di Blanco, Y. E., De Angelo, C. D., and Di Bitetti, M. S. (2009). Protection affects the abundance and activity patterns of pumas in the Atlantic Forest. *Journal of Mammalogy* **90**, 926–934. doi:10.1644/08-MAMM-A-128.1
- Payton, M. E., Greenstone, M. H., and Schenker, N. (2003). Overlapping confidence intervals or standard error intervals: what do they mean in terms of statistical significance? *Journal of Insect Science* **3**, 1–6. doi:10.1673/031.003.3401
- Pierce, B. M. (2000). Selection of mule deer by mountain lions and coyotes: effects of hunting style, body size, and reproductive status. *Journal of Mammalogy* **81**, 462–472. doi:10.1644/1545-1542(2000)081<0462:SO MDBM>2.0.CO;2
- Plummer, M., Best, N., Cowles, K., and Vines, K. (2006). CODA: convergence diagnosis and output analysis for MCMC. *R News* **6**, 7–11.
- Quiroga, V. a., Noss, A. J., Paviolo, A., Boaglio, G. I., and Di Bitetti, M. S. (2016). Puma density, habitat use and conflict with humans in the Argentine Chaco. *Journal for Nature Conservation* **31**, 9–15. doi:10.1016/j.jnc.2016.02.004
- R Development Core Team (2013). 'R: a Language and Environment for Statistical Computing.' Available at [www.R-project.org](http://www.R-project.org) [Verified 28 August 2016]
- Ray, J., Redford, K., Steneck, R., and Berger, J. (2005). 'Large Carnivores and the Conservation of Biodiversity.' (Island Press: Washington, DC.)
- Rich, L. N., Kelly, M. J., Sollmann, R., Noss, A. J., Maffei, L., Arispe, R. L., Paviolo, A., De Angelo, C. D., Di Blanco, Y. E., and Di Bitetti, M. S. (2014). Comparing capture-recapture, mark-resight, and spatial mark-resight models for estimating puma densities via camera traps. *Journal of Mammalogy* **95**, 382–391. doi:10.1644/13-MAMM-A-126
- Ridout, M. S., and Linkie, M. (2009). Estimating overlap of daily activity patterns from camera trap data. *Journal of Agricultural Biological & Environmental Statistics* **14**, 322–337. doi:10.1198/jabes.2009.08038
- Robinson, H. S., Wielgus, R. B., Cooley, H. S., and Cooley, S. W. (2008). Sink populations in carnivore management: cougar demography and immigration in a hunted population. *Ecological Applications* **18**, 1028–1037. doi:10.1890/07-0352.1
- Robinson, H. S., Desimone, R., Hartway, C., Gude, J. a., Thompson, M. J., Mitchell, M. S., and Hebblewhite, M. (2014). A test of the compensatory mortality hypothesis in mountain lions: a management experiment in west-central Montana. *The Journal of Wildlife Management* **78**, 791–807. doi:10.1002/jwmg.726
- Royle, J. A., Nichols, J. D., Karanth, K. U., and Gopalaswamy, A. M. (2009). A hierarchical model for estimating density in camera trap studies. *Journal of Applied Ecology* **46**, 118–127. doi:10.1111/j.1365-2664.2008.01578.x
- Royle, J. A., Chandler, R. B., Sollmann, R., and Gardner, B. (2014). 'Spatial Capture-recapture.' (Academic Press: Waltham, MA.)
- Silveira, L., Jacomo, A. T. A., and Diniz-Filho, J. A. F. (2003). Camera trap, line transect census and track surveys: a comparative evaluation. *Biological Conservation* **114**, 351–355. doi:10.1016/S0006-3207(03)00063-6
- Sollmann, R., Gardner, B., Chandler, R. B., Shindle, D. B., Onorato, D. P., Royle, J. A., and O'Connell, A. F. (2013a). Using multiple data sources provides density estimates for endangered Florida panther. *Journal of Applied Ecology* **50**, 961–968. doi:10.1111/1365-2664.12098
- Sollmann, R., Gardner, B., Parsons, A. W., Stocking, J. J., McClintock, B. T., Simons, T. R., Pollock, K. H., and O'Connell, A. F. (2013b). A spatial mark-resight model augmented with telemetry data. *Ecology* **94**, 553–559. doi:10.1890/12-1256.1
- Soria-Díaz, L., Monroy-Vilchis, O., Rodríguez-Soto, C., Zarco-González, M., and 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.
- Stoner, D. C., Wolfe, M. L., and Choate, D. M. (2006). Cougar exploitation levels in Utah: implications for demographic structure, population recovery, and metapopulation dynamics. *The Journal of Wildlife Management* **70**, 1588–1600. doi:10.2193/0022-541X(2006)70[1588:CELIUI]2.0.CO;2
- Sunquist, M., and Sunquist, F. (2002). 'Wild Cats of the World.' (The University of Chicago Press: Chicago, IL.)
- Treves, A. (2009). Hunting for large carnivore conservation. *Journal of Applied Ecology* **46**, 1350–1356. doi:10.1111/j.1365-2664.2009.01729.x
- Treves, A., and Karanth, K. U. (2003). Human-carnivore conflict and perspectives on carnivore management worldwide. *Conservation Biology* **17**, 1491–1499. doi:10.1111/j.1523-1739.2003.00059.x
- Van Schaik, C. P., and Griffiths, M. (1996). Activity periods of Indonesian rain forest mammals. *Biotropica* **28**, 105–112. doi:10.2307/2388775
- Walker, S., and Novaro, A. (2010). The world's southernmost pumas in Patagonia and the southern Andes. In 'Cougar: Ecology and Conservation'. (Eds M. Hornocker and S. Negri.) pp. 91–99. (University of Chicago Press: Chicago, IL.)
- White, G. C., and Shenk, T. M. (2001). Population estimation with radio-marked individuals. In 'Radio Tracking and Animal Populations'. (Eds J. Millspaugh and J. M. Marzluff.) pp. 329–350. (Academic Press: San Diego, CA.)
- Wilson, K. R., and Anderson, D. R. (1985). Evaluation of a nested grid approach for estimating density. *The Journal of Wildlife Management* **49**, 675–678. doi:10.2307/3801693
- Wilson, D. E., and Mittermeier, R. A. (2009). 'Handbook of the Mammals of the World. Vol. 1. Carnivores.' (Lynx Edicions: Barcelona, Spain.)
- Woodroffe, R., and Ginsberg, J. (1998). Edge effects and the extinction of populations inside protected areas. *Science* **280**, 2126–2128. doi:10.1126/science.280.5372.2126
- Zanón Martínez, J. I., Travaini, A., Zapata, S., Procopio, D., and Santillán, M. Á. (2012). The ecological role of native and introduced species in the diet of the puma *Puma concolor* in southern Patagonia. *Oryx* **46**, 106–111. doi:10.1017/S0030605310001821
- Zanón Martínez, J. I., Santillán, M. Á., Sarasola, J. H., and Travaini, A. (2016). A native top predator maintained by exotic preys inside a protected area: the puma and the introduced ungulates. *Journal of Arid Environments* **134**, 17–20. doi:10.1016/j.jaridenv.2016.06.015