

Density and activity patterns of Andean cat and pampas cat (*Leopardus jacobita* and *L. colocolo*) in the Bolivian Altiplano

Juan Carlos Huaranca^{A,B,C,I}, Ma. Lilian Villalba^B, Nuno Negrões^D,
Jaime E. Jiménez^{A,E}, David W. Macdonald^F and Luis F. Pacheco^{G,H}

^APrograma de Doctorado en Ciencias, mención Conservación y Manejo de Recursos Naturales, Universidad de Los Lagos, Avenida Fushlocher 1305, Osorno, Chile.

^BAndean Cat Alliance, www.gatoandino.org.

^CCentro de Biodiversidad y Genética, Universidad Mayor de San Simón, Calle Sucre frente al Parque La Torre, Cochabamba, Bolivia.

^DCESAM and Departamento de Biología, Universidade de Aveiro, Campus Universitário de Santiago 3810-193, Aveiro, Portugal.

^EDepartment of Biological Sciences, Advanced Environmental Research Institute, University of North Texas, College of Science, TX 76203, USA.

^FWildlife Conservation Research Unit, Department of Zoology, The Reanati-Kaplan Centre, University of Oxford, Tubney House, Abingdon Road, Tubney, Abingdon, OX13 5QL, UK.

^GColección Boliviana de Fauna, Instituto de Ecología, Carrera de Biología, Universidad Mayor de San Andrés, Calle 27 Cota Cota, La Paz, Bolivia.

^HCentro de Estudios en Biología Teórica y Aplicada, BIOTA, Avenida Las Retamas No. 15, entre Calles 34 y 35, La Paz, Bolivia.

^ICorresponding author. Email: jchuaranca@gmail.com

Abstract

Context. Understanding the factors that determine the distribution and abundance of species is an important aim of ecology and prerequisite for conservation. The Andean cat (*Leopardus jacobita*) and the pampas cat (*L. colocolo*) are two of the least studied felids. Both are threatened, of similar size and live sympatrically in the Andes of Argentina, Bolivia, Chile, and Perú.

Aims. We aimed at estimating the population densities of the Andean cat and pampas cat in two continuous areas and to analyse the activity patterns of these two species and that of mountain vizcacha (*Lagidium viscacia*), the main prey of the Andean cat.

Methods. We used camera traps to evaluate the density of both felid species using the space explicit capture recapture (SECR) framework and the overlap in their activity patterns with that of mountain vizcacha, using the kernel-density estimator in two contiguous areas in the Bolivian Altiplano, at Muro-Amaya and at Micani, both within the Ciudad de Piedra region.

Key results. Andean cat density was estimated at 6.45 individuals per 100 km² in Muro-Amaya and 6.91 individuals per 100 km² in Micani, whereas the density of the pampas cat was 5.31 individuals per 100 km² and 8.99 individuals per 100 km² respectively. The Andean cat was mainly nocturnal, whereas the pampas cat was cathemeral. The activity of the mountain vizcacha overlapped less with that of its specialised predator, the Andean cat, than with that of the pampas cat.

Conclusions. In line with our predictions, the Andean cat, considered a more specialised nocturnal hunter, particularly of mountain vizcacha, had lower population densities than did the more generalist pampas cat.

Implications. Low population densities, as compared with theoretical expectations, pose an additional conservation problem for these felids, in an area such as the high Andes.

Additional keywords: camera-trapping, endangered species, generalist species, overlap, spatially explicit capture–recapture, specialist species.

Received 19 March 2019, accepted 6 September 2019, published online 18 December 2019

Introduction

The paucity of data on the ecology of small felids, population density and distribution hampers our understanding of their biology and obscures their conservation status (Nowell and Jackson

1996; Yensen and Seymour 2000; Lucherini *et al.* 2008; Macdonald and Loveridge 2010). This is a handicap for conservation planning. Often, there are differences in the density estimation of small cats at different sites for the same species, mainly

due to habitat characteristics or the availability of resources (Riley 2006). Camera-trapping surveys have been used in the past decade to estimate the population size of wild species, the inter- and intraspecific interactions, and the activity patterns of these species as well as those of their prey (e.g. Suraci *et al.* 2017). This technique is especially useful for studying species that are cryptic, rare and live in remote areas, as well as to examine predator–prey interactions (Foster *et al.* 2013). In the Espinal of central Argentina, Geoffroy's cat (*Leopardus geoffroyi*) has a higher density than does the pampas cat (*L. colocolo*; Caruso *et al.* 2012). The activity of the guíña (*L. guigna*) overlapped closely with that of small mammals, but not with two bird species considered to be its main prey (Delibes-Mateos *et al.* 2014).

In Bolivia, where nine little-known felids occur only, a handful of studies have been conducted on small sympatric carnivores (Noss *et al.* 2012) and four species of small cats (Arispe *et al.* 2007). Two of the least studied felid species occur in the highlands of the Bolivian Altiplano, namely, the Andean cat (*L. jacobita*), which is categorised as *Critically Endangered* in Bolivia (Villalba *et al.* 2009a) and as *Endangered* by IUCN (Villalba *et al.* 2016), and the pampas cat (*L. colocolo*), which is classified as *Vulnerable* in Bolivia (Villalba *et al.* 2009c), and *Near Threatened* by IUCN (Lucherini *et al.* 2016). Andean and pampas cats are often sympatric in high Andean regions of Argentina, Bolivia, Chile and Perú, and in the northern Patagonian steppe (Nowell and Jackson 1996; Marino *et al.* 2011; Lucherini *et al.* 2016; Villalba *et al.* 2016). Both species are among the least studied felids, with scant information being available on their natural history, abundances and ecologies (Marino *et al.* 2010). The only previous information on these species in Bolivia comes from the Eduardo Avaroa Andean Fauna National Reserve where, using radio-tracking, Villalba *et al.* (2009b) estimated the home ranges of a female Andean cat and a female pampas cat (65.5 km² and of 55.3 km² respectively). Additionally, two unpublished studies (Viscarra 2008; Torrico 2009) have reported on the diets and relative abundances of the sympatric Andean cat, pampas cat and culpeo fox (*Lycalopex culpaeus*) in the same reserve. Viscarra (2008) and Torrico (2009) found that the Andean cat diet is composed mainly of mountain vizcacha (*Lagidium viscacia*), supporting the hypothesis that this is a specialist vizcacha hunter (Marino *et al.* 2010). Conversely, the pampas cat is considered a dietary generalist, eating mainly small rodents, along with mountain vizcachas (4–29% of its prey items), birds and lizards (Walker *et al.* 2007; Napolitano *et al.* 2008; Fajardo *et al.* 2014).

Under the assumption that Andean and pampas cats rely significantly on mountain vizcachas, we sought to document their activity patterns in relation to that of this prey. Mountain vizcachas are active mainly at dawn and dusk, but are often active at night (Tarifa and Yensen 2001). Although there is scant information on the behaviour of both felid species, we would predict that their activity patterns would be coupled with that of vizcachas. However, we hypothesise that, given the greater feeding specialisation of Andean cats on mountain vizcachas, the activity patterns between these two species would show a greater overlap than the activity patterns between pampas cat and mountain vizcachas.

Body size is an important parameter explaining spatial use and abundance patterns in mammals (McNab 1963; Carbone and

Gittleman 2002). The Andean cat and pampas cat differ little in morphology, except that the Andean cat is slightly larger (weight: 5.16 ± 0.09 kg) than the pampas cat (3.52 ± 0.13 kg; Tellaeche 2015). Accordingly, densities of Andean cat reported in Argentina are lower (from 7 individuals per 100 km², CI 95% 4–15, to 12 individuals per 100 km², CI 95% 8–23; Reppucci *et al.* 2011) than those for pampas cat at the same sampling sites (from 74 individuals per 100 km², CI 95% 26–148, to 78 individuals per 100 km², CI 95% 32–146; Gardner *et al.* 2010). A preliminary report using minimum numbers known alive from our study site, Ciudad de Piedra (Bolivia), also yielded a slightly lower density estimate of (1.8 individuals per 100 km²) for the Andean cat than for the pampas cat (4.9 individuals per 100 km²; Huaranca *et al.* 2013). In the present study, we provide abundance estimates for these two cat species, based on a longer study at Ciudad de Piedra (Stone city), in the south-west of La Paz Department (Huaranca *et al.* 2013). On the basis of the differences in body size between the cats, we predicted that the density of the pampas cat would be higher than that of the Andean cat. We provide information on the abundance and activity patterns of both species at a site previously argued to be of utmost importance for their conservation (Huaranca *et al.* 2013).

Materials and methods

Study area

Ciudad de Piedra is a continuous rocky landscape, resulting from volcanic activity, located in the south-west of the La Paz Department, Bolivia, near the borders with Chile and Perú (17°32'S, 68°51'W), ranging between 3900 and 4035 m a.s.l. The area is topographically complex, with deep rocky canyons. Canyons may reach 120 m in depth, and 800 m wide at their entrances. People inhabit some of the lower ranges of the canyons, but human density is low (2.53 inhabitants km⁻²; Gobierno Autónomo Municipal de Calacoto 2008). Camelid livestock (mainly lamas, *Lama glama*) roam throughout the area, but they usually remain close to human settlements, which are, in turn, located close to roads, generally in flatter areas and at lower elevations (Huaranca *et al.* 2013).

Ciudad de Piedra covers ~1500 km² of well preserved wildlife habitats (Huaranca *et al.* 2013). Average annual temperature is 7°C, with extremes of 27°C in the rainy season and -15°C in the dry season. Annual precipitation averages 450 mm and falls mainly between December and March. The soil in the area is generally poor in nutrients, but the local flora and fauna, particularly the birds and mammals, are among the most diverse of the Bolivian Altiplano (Huaranca and Villalba 2011). Main human activities at Ciudad de Piedra area are subsistence agriculture (particularly growing potatoes), and livestock husbandry (7440 lamas and 1674 cattle; Gobierno Autónomo Municipal de Calacoto 2008). We evaluated two areas within Ciudad de Piedra, namely, Muro-Amaya and Micani. Muro-Amaya is characterised by the presence of permanent streams running through the canyon, bordered by hillsides with slopes between 15° and 70°. These slopes harbor a rich flora (86 recorded species), with Asteraceae, Poaceae and Solanaceae being the most diverse families (Teran and Huaranca 2012). The Micani area, 10 km south-west in a straight line from Muro-Amaya, is characterised by having seasonal streams, steeper slopes (45–90°), and a less

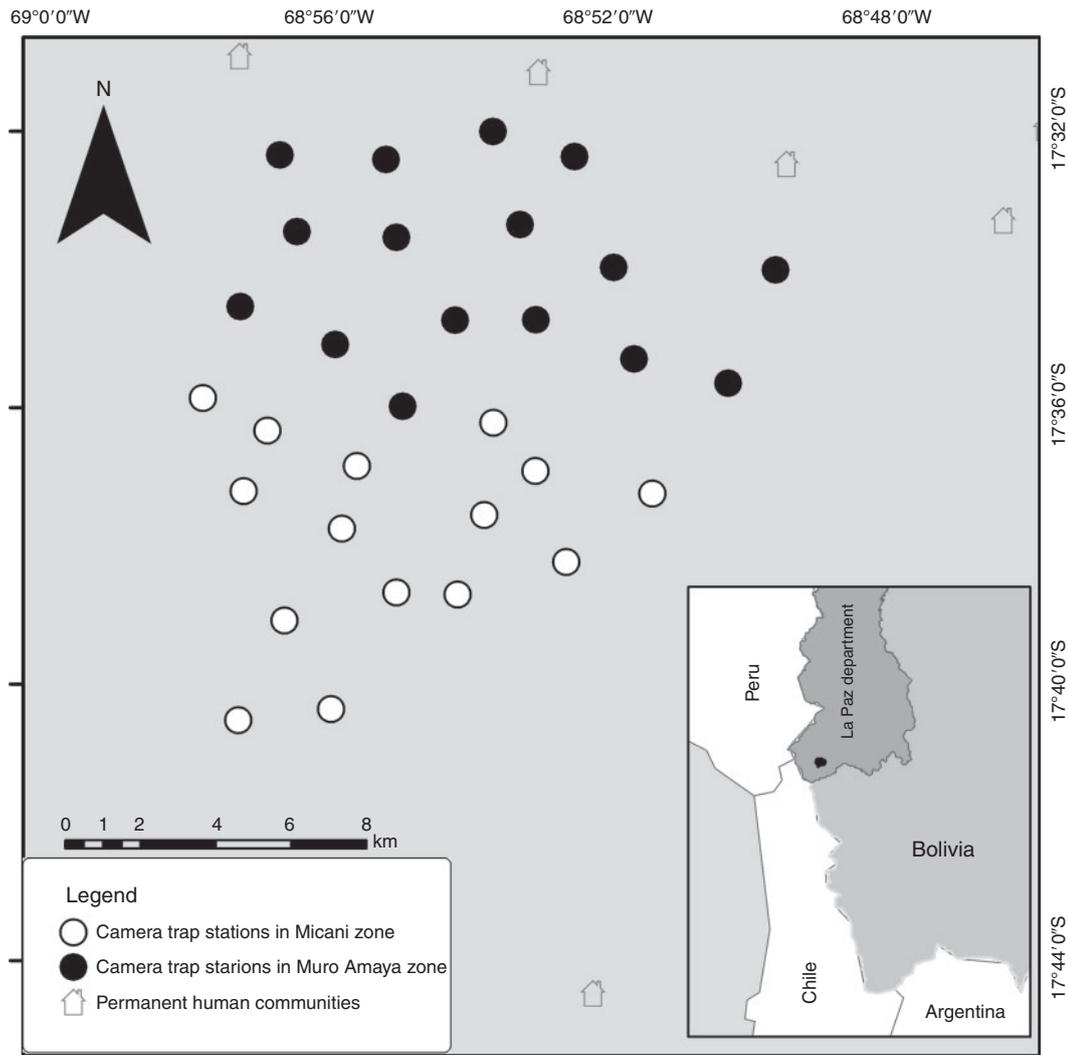


Fig. 1. Distribution of camera-trap stations in the two sampled areas within Ciudad de Piedra, La Paz Department, western Bolivia. Sampling at Muro-Amaya was run between September 2011 and January 2012 and that at Micani between September 2012 and January 2013.

diverse flora, where Asteraceae is the most diverse family, followed by Fabaceae and Solanaceae (Teran and Huaranca 2012). Human presence at Micani is only sporadic, whereas people are residents in Muro-Amaya.

Sampling methods

We sampled in two spatially continuous areas between 2011 and 2013, covering 216 km² in the north-eastern and central areas of Ciudad de Piedra (Fig. 1). At Muro-Amaya, sampling was conducted from September 2011 through to January 2012, whereas at Micani it was from September 2012 through to January 2013. Both sampling periods were conducted between the end of the dry season and the beginning of the humid season. At each site, we installed a total of 31 camera stations spaced at 2.5–3.0 km, using two cameras per station. The spacing was calculated as the radius of the home range of a female Andean cat (Balme *et al.* 2009; Villalba *et al.* 2009b), following the protocols of Cossios *et al.* (2007) and Reppucci *et al.* (2011).

Cameras were placed 50 cm above the ground and set on each side of trails likely to be used by cats, and they were programmed to operate continuously and were checked every 30 days for a total of ~140 days.

Density estimates

Identification of individuals was based on the specific lateral-spot patterns, tail rings (in the case of Andean cat), and the rings in the front legs (for pampas cat). We built a capture–recapture matrix for each species for each area, and used the spatially explicit capture–recapture (SECR) framework (Borchers and Efford 2008; Royle and Gardner 2011; Noss *et al.* 2012; Sollmann *et al.* 2012). The SECR model uses the spatial information of the capture–recapture data to estimate the distribution of animals in space, and their density. It assumes that animals have fixed circular home ranges and that the photographic capture rate declines with distance from the activity centre (home-range geometric centre), following a specific detection

function. We also assumed that the number of individuals (i) photographed at a camera station (j) and on occasion k , Y_{ijk} , had a Poisson distribution, with a mean encounter rate of λ_{ijk} (for more details of the model, see Royle and Gardner 2011). The most commonly used detection function in SECR is the half-normal function that has two parameters, namely, the encounter rate at the home-range geometric centre λ_0 (i.e. the expected number of captures in a trap, given that the activity is centred at the trap), and the scale parameter σ that describes how the encounter rate decreases with an increasing distance from the home-range geometric centre. The detection function is also related to the home-range radius (Royle *et al.* 2009; Zanón-Martínez *et al.* 2016). We used the maximum-likelihood framework (Efford *et al.* 2009) to estimate population densities. The Poisson encounter model was used to estimate the probability of detecting an individual. These models have proved useful in several carnivore-sampling studies, including small cats, as demonstrated by Gardner *et al.* (2010) and Reppucci *et al.* (2011). Here, we use the SECR maximum likelihood approach (ML SECR), because it estimates the density and size of a spatially distributed animal population sampled with passive detectors, such as camera traps. The ML SECR models include prediction factors of the detection probability including both the predefined variables corresponding to time and behaviour and user-defined variables such as habitat masks (Borchers and Efford 2008). Given that our sampling intervals lasted more than 90 days, we evaluated whether the populations complied with the assumption of closure, using the command closure test of the *secr* package in R (Efford 2014). We evaluated the models in relation to the sources of variation in the probability of capture that is considered in the capture–recapture models as follows: the null model (*secr0*), in which the probability of capture is the same for all individuals on all the occasions; the model of behaviour (*secrb*) that assumes the differences in the probability of capture due to behaviour; the individual heterogeneity model (*secrh2*) that assumes that there are differences in the probability of capture between individuals; the model of behaviour and time (*secrbT*) that sums differences in the probabilities of capture due to the behaviour and the sampling time; the model of variation over time (*secrT*) that assumes that there are differences in the probability of capture owing to the sampling time; and the model that assumes that the capture probability varies with behaviour and time, affecting the λ_0 and σ parameters (*secrlist*). The model selection was run using the Akaike information criteria (AIC) approach, for each species in each population density-assessment site (Efford 2014). Spatially explicit capture–recapture analyses were performed using the *secr* package (Efford 2014) in software R (R Core Team 2016).

Activity patterns

To study daily activity patterns, we used the time information from the photographic records of Andean cat, pampas cat and mountain vizcacha from both camera-trapping sampling areas. To avoid autocorrelation, we used only photographs of the same species from the same camera that were obtained >1 h apart, except when we could identify distinct individuals (Linkie and Ridout 2011; Foster *et al.* 2013; Zanón-Martínez *et al.* 2016).

Activity patterns were included in one of the following time categories: (1) diurnal, active between 1 h after sunrise and 1 h

before sunset; (2) nocturnal, active between 1 h after sunset and 1 h before sunrise; (3) dawn, active from 1 h before to 1 h after sunrise, and (4) dusk, active from 1 h before to 1 h after sunset (Theuerkauf *et al.* 2003b). We used log-likelihood ratio tests to determine whether activity for each species was homogeneously distributed across those periods and to compare activity patterns among species. To avoid an excess of small (<5) expected values, data from dawn and dusk were pooled for these tests as ‘crepuscular,’ because these two periods had small samples sizes and similar light conditions (Lucherini *et al.* 2009). The timing records for each species were transformed into circular time and then analysed using the kernel-density method to describe the patterns of activity of the species and to estimate the coefficient of overlap (Δ_1 ; Ridout and Linkie 2009). This coefficient ranges from 0 (no overlap) to 1 (complete overlap) and is calculated as the area under the curve that is formed by superimposing the activity-pattern areas for the two species under comparison. Finally, we obtained the 95% confidence intervals (CIs) for these estimates from bootstrap re-sampling 5000 times. All statistics were analysed using the *overlap* package (Ridout and Linkie 2009) in R (R Core Team 2016).

Results

Sampling effort at Muro-Amaya was 2313 camera-trap days and resulted in 19 Andean cat events (eight individuals), 28 pampas cat events (10 individuals) and 508 mountain vizcachas events. A sampling effort of 2136 camera-trap days in the Micani area gave 18 Andean cat events (seven individuals), 18 pampas cat events (six individuals) and 426 mountain vizcacha events.

Density estimates

The area covered by camera traps was 188 km² at Muro-Amaya and 101 km² at Micani. Populations were closed during the period of sampling for all cases, except for the Andean cat at the Micani area ($P = 0.02$). The best model for the population-density estimation of the Andean and pampas cats was the null model (*secr0*), where the probability of capture is the same for all individuals at all times (Table 1). The spatial parameter (σ) was 1.46 (± 0.39) km for the Andean cat and 1.77 (± 0.31) km for the pampas cat in Muro-Amaya. At Micani, it was 1.31 (± 0.24) km for the Andean cat and 0.61 (± 0.12) km for the pampas cat (Table 1). Andean cat-density estimate was 6.45 (± 2.9) individuals per 100 km² in Muro-Amaya and 6.91 (± 3.08) individuals per 100 km² in Micani, whereas the density of the pampas cat was 5.31 (± 2.02) individuals per 100 km² and 8.99 (± 4.54) individuals per 100 km² in Muro-Amaya and Micani respectively (Table 1). The basal encounter-rate (λ_0) estimations for Andean cat (0.108 and 0.107 for Muro-Amaya and Micani respectively) were lower than for pampas cat (0.174 and 0.609 for Muro-Amaya and Micani respectively) in both areas.

Activity patterns

We pooled data from both sampling areas, resulting in 1017 records for all three species (36 for Andean cat, 46 for pampas cat, and 934 for vizcacha). All three species were mainly nocturnal (42.5% of all events), followed by diurnal (32.9%) and crepuscular activity (24.6%; Fig. 2). The Andean cat was more active at night (72.9% of the events) than both the pampas

Table 1. Density estimates for Andean cat (*Leopardus jacobita*) and pampas cat (*L. colocolo*) in Muro-Amaya and Micani areas of Ciudad de Piedra, western Bolivia

AIC ω , weight of the Akaike information criterion for the secr0 model; number of individuals, the number of cats captured in the sampling; D , density estimated; λ_0 , expected number of encounters per interval for an individual with an activity centre located at a given trap; σ , shape parameter in the detectability function; and CI, the 95% confidence interval. Standard errors are given in parentheses

Species	Location	AIC ω secr0 model	Number of identified individuals	D (individuals per 100 km ²)	CI 95%	λ_0 (km)	σ (km)
Andean cat	Muro-Amaya	0.981	8	6.45 (2.90)	2.77–14.49	0.108 (0.55)	1.46 (0.39)
	Micani	0.992	7	6.91 (3.08)	2.99–15.95	0.107 (0.49)	1.32 (0.26)
Pampas cat	Muro-Amaya	0.897	10	5.31 (2.02)	2.59–10.92	0.174 (0.64)	1.77 (0.31)
	Micani	1.000	6	8.99 (4.54)	3.53–22.90	0.609 (2.36)	0.61 (0.12)

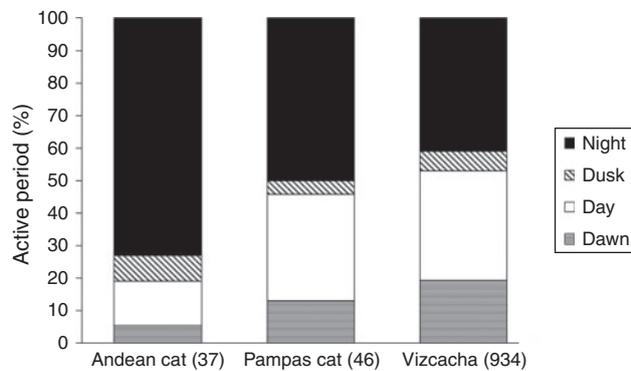


Fig. 2. Activity patterns of the Andean cat, pampas cat and mountain vizcacha, represented as the number of independent detections (events h⁻¹) occurring within each of the four periods of the 24-h day cycle at Ciudad de Piedra, western Bolivia. The number of independent events is shown in parenthesis.

cat (50% of events) and the mountain vizcacha (40.9% of events). The Andean cat was equally active during the day (13.5%) and during the crepuscular periods (13.5%), whereas, for the pampas cat, the second most active period was during the day (32.6%). The crepuscular activity of the mountain vizcacha (25.4% of the events) was 1.5 times that of the pampas cat (17.4% of the events; Fig. 2). We found no significant differences in the coefficient of overlap between pairs of species. The lowest coefficient of overlap (Δ^1) for activity patterns was 0.66 (CI = 0.44–0.73) between the Andean cat and mountain vizcacha, as compared with 0.83 (CI = 0.66–0.85) between the pampas cat and mountain vizcacha, and 0.75 (CI = 0.62–0.83) between the Andean cat and pampas cat (Fig. 3).

Discussion

Density estimates

Our density estimates were slightly higher than the preliminary figures we reported for both species at the same study site (Huaranca *et al.* 2013). These preliminary estimates followed the expected trend of a higher density for the pampas cat than that for Andean cat, whereas the ones we have reported here fulfilled this expectation for only one of the sampling sites. The differences in densities between our previous estimates and the present study may be due to the more intense sampling effort, a larger sampled area and the use of a more robust method for

density estimation in the current study (Noss *et al.* 2012; Ivan *et al.* 2013). However, we cannot rule out the possibility that the differences reflect real changes in abundance.

The assumption of a closed population was met for the pampas cat in both sampling areas and for the Andean cat only for the Muro-Amaya area. Although we recognise this weakness in the estimation of the Andean cat population in the Micani area, the inaccuracy may be minor. Yearly survival in other small to medium-sized felid species within unharvested populations is usually below 17% (Haines *et al.* 2004; Blankenship *et al.* 2006; López *et al.* 2014), but can be as high as 23% in *L. geoffroyi* (Pereira 2009). Hence, assuming a yearly mortality rate of 20%, we would expect a <10% of mortality within our sampling period of 140 days, resulting in a fairly small bias in our density estimate of Andean cat at Micani.

Although the confidence intervals for pampas cat overlapped, mean population densities differed between Micani and Muro-Amaya areas, which suggests a potential difference in the habitats. Given that both felids share similar prey (overlapping up to 82% in prey biomass; Napolitano *et al.* 2008), the differences in the density of pampas cat between the sites may be explained by differences in the abundances of prey between the sites. Accordingly, the number of vizcachas recorded in camera traps was higher at Muro-Amaya than at Micani. However, it is intriguing that Andean cat densities between these sites were similar.

We highlight the differences in pampas cat density estimates from Jujuy province in Argentina and Ciudad de Piedra. One simple explanation may be a difference in productivity between these sites (Santini *et al.* 2018). The differences in the diversity of plants between these two areas might affect food availability for the main herbivorous prey (Jones and Dayan 2000; Kolowski and Woolf 2002; Ross *et al.* 2013), but we do not have data to test this hypothesis. However, it is unlikely that a difference in productivity can explain such a large difference in the density of the pampas cat between the sites (5.31–8.99 individuals per 100 km² at Ciudad de Piedra vs 74–78 individuals per 100 km² in Jujuy; Gardner *et al.* 2010). We strongly suspect of an undetected methodological bias. However, our estimate for pampas cat is much closer to a previous estimate (11.37 individuals per 100 km²) for Buenos Aires province, located in the transition zone between the pampas grasslands and the Argentine Monte (Caruso *et al.* 2012).

It is known that the spacing of cameras may affect density estimates (Balme *et al.* 2009; Noss *et al.* 2012) and the size of the

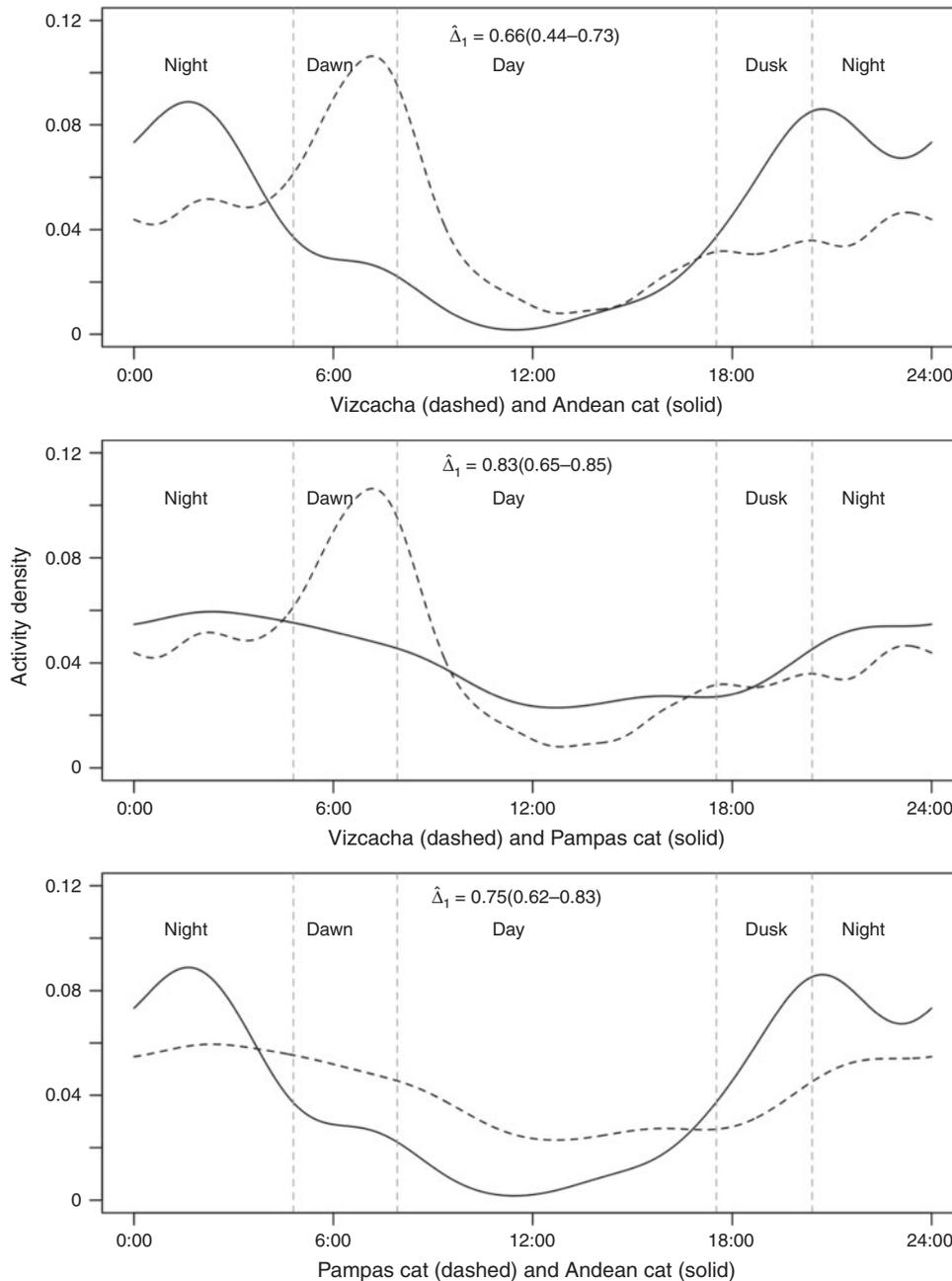


Fig. 3. Overlaps of daily activity patterns among Andean cat and pampas cat, and mountain vizcacha, their main prey, in western Bolivia. The overlap coefficients are represented by the area under both curves. Δ is the coefficient of overlap, the subscript 1 is the best estimator for small sample sizes. Day, active between 1 h after sunrise and 1 h before sunset; night, active between 1 h after sunset and 1 h before sunrise; dawn, active from 1 h before to 1 h after sunrise, and dusk, active from 1 h before to 1 h after sunset.

sampling area can affect the results, such that larger sampled areas usually result in lower estimates (Silva *et al.* 2001).

Overall, the estimated densities for both species were low, as compared with theoretical expectations. Using the equation proposed by Carbone and Gittleman (2002), the expected density for a felid the size of an Andean cat (around 5 kg) would be ~ 47 individuals per 100 km², which is 4–7 times greater than was our estimate (Reppucci *et al.* 2011; this study). Again, this may be

due to the fact that Andean cat inhabits environments low in productivity (Santini *et al.* 2018), which is further evidenced by the apparently very large home ranges of 65.52 km² (for Kernel 95%) of an individual in southern Bolivia (Villalba *et al.* 2009b), and of 46.89 km² (mean Kernel 95%) of three individuals in northern Argentina (Tellaecche 2015), which, on the basis of body-size allometry, might have been expected to be closer to 5 km² (Kelt and Van Vuren 2001).

Activity patterns

The daily activity patterns of Andean and pampas cats at Ciudad de Piedra are apparently similar, reaching 75% of overlap, with the pampas cat being slightly more active during the day than the Andean cat, and *vice versa* by night. Villalba *et al.* (2009b) reported that the Andean cat is more active during the night and less active in crepuscular (dawn and dusk) and day periods, which is similar to our findings. However, we found that the Andean cat was more nocturnal in Ciudad de Piedra (73%) than was reported by Lucherini *et al.* (2009) for 13 sites in Argentina, Bolivia and Chile. For the pampas cat, Villalba *et al.* (2009b) documented that it is active throughout the day, whereas Lucherini *et al.* (2009) reported it to be mostly nocturnal, which agrees with the results from our sites. Although, the Andean cat is thought to feed mainly on mountain vizcachas (Walker *et al.* 2007; Napolitano *et al.* 2008; Villalba *et al.* 2009d), we found greater congruence between the activity patterns of pampas cats and mountain vizcachas, which can be interpreted as a shift of the temporal niche of the vizcacha driven by the presence of the Andean cat. It is possible that temporal niche partitioning may be occurring between pampas and Andean cats, as reported for other species living in sympatry (Santos *et al.* 2019).

Insofar as the activities of Andean and pampas cats overlap widely in time and space, this raises the possibility that they lower competition on another niche axis, as might be expected under the niche complementarity hypothesis (Schoener 1974; Jiménez *et al.* 1996). Furthermore, little is known about the competitive dynamics among other guild members, including the culpeo fox, the puma and the lesser grison (*Galictis cuja*). If the low population densities of these two felids are both below their carrying capacity, this might facilitate coexistence. Together, their aggregate densities fall in the range of 11.7–15.9 cats per 100 km² at Ciudad de Piedra. That is 30% of the density estimated allometrically for a ‘typical’ 5-kg cat, according to Carbone and Gittleman (2002).

Our data have added evidence to the conclusion that felid species inhabiting the high Andes have population densities much lower than expected for a carnivore of their size, particularly for Andean cats. Additionally, at least Andean cats seem to have a very patchy distribution, related to areas covered mostly by rocky habitat, as mentioned by Napolitano *et al.* (2008) and Marino *et al.* (2010). These findings have important implications for their conservation, because Andean cats, but also pampas cats, may need very large areas to maintain viable populations. This may pose an additional problem for the conservation of these felid species. Even though our study area has a low human population density, the Andean region, in general, is highly degraded by intensive agriculture and livestock-raising activities, as well as by mining operations. However, our study area encompasses a large expanse of rocky habitats, highly suitable for both felid species (Huaranca *et al.* 2013).

Conflicts of interest

The authors declare no conflicts of interest.

Acknowledgements

We acknowledge the collaboration of indigenous authorities of Ayllu Pahaza, and the Municipality of Calacoto. This research was funded by

Wildlife Conservation Network, Small Cats Action Fund (Panthera Foundation), Mohamed bin Zayed Species Conservation Fund (Project: 11053162), and Iniciativa de Especies Amenazadas Becas ‘Werner Hanagarth’ (Fundación Puma). We also want to thank the support granted by the Andean Cat Alliance, ESRI Conservation Program, Idea Wild, Instituto de Ecología at Universidad Mayor de San Andrés, and the Wildlife Conservation Society of Bolivia. Our thanks also go to Alejandra Torrez for her constant support. Herminio Ticona, Jim Sanderson, Miguel Saavedra, Mauricio Peñaranda, Yony Quiñones, and Gregorio Roque helped during fieldwork. We are grateful to Susan Walker for helpful comments on a previous version of this manuscript and two anonymous reviewers provided useful comments to the previous version of this manuscript.

References

- Arispe, R., Rumiz, D., and Noss, A. (2007). Six species of cats registered by camera trap surveys of tropical dry forest in Bolivia. *Cat News* **46**, 36–38.
- Balme, G. A., Hunter, L. T. B., and Slotow, R. (2009). Evaluating methods for counting cryptic carnivores. *The Journal of Wildlife Management* **73**, 433–441. doi:10.2193/2007-368
- Blankenship, T. L., Haines, A. M., Tewes, M. E., and Silvy, N. J. (2006). Comparing survival and cause-specific mortality between resident and transient bobcats *Lynx rufus*. *Wildlife Biology* **12**, 297–303. doi:10.2981/0909-6396(2006)12[297:CSACMB]2.0.CO;2
- 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
- Carbone, C., and Gittleman, J. L. (2002). A common rule for the scaling of carnivore density. *Science* **295**, 2273–2276. doi:10.1126/science.1067994
- Caruso, N., Manfredi, C., Vidal, E. M. L., Casenave, E. B., and Lucherini, M. (2012). First density estimation of two sympatric small cats, *Leopardus colocolo* and *Leopardus geoffroyi*, in a shrubland area of central Argentina. *Annales Zoologici Fennici* **49**, 181–191. doi:10.5735/086.049.0306
- Cossíos, D., Beltran-Saavedra, F., Bennet, M., Fajardo, U., Lucherini, M., Merino, M. J., Marino, J., Napolitano, C., Palacios, R., Perovic, P., Ramirez, Y., Villalba, L., Walker, S., and Sillero-Zubiri, C. (2007). ‘Manual de Metodologías para Relevamiento de Carnívoros Alto Andinos.’ (Alianza Gato Andino: Buenos Aires, Argentina.)
- Delibes-Mateos, M., Díaz-Ruiz, F., Caro, J., and Ferreras, P. (2014). Activity patterns of the vulnerable guinea (*Leopardus guigna*) and its main prey in the Valdivian rainforest of southern Chile. *Mammalian Biology. Zeitschrift für Säugetierkunde* **79**, 393–397.
- Efford, M. (2014). Bias from heterogeneous usage of space in spatially explicit capture–recapture analyses. *Methods in Ecology and Evolution* **5**, 599–602. doi:10.1111/2041-210X.12169
- Efford, M. G., Borchers, D. L., and Byrom, A. E. (2009). Density estimation by spatially explicit capture–recapture: likelihood-based methods. In ‘Modeling Demographic Processes in Marked Populations’. (Eds D. L. Thomson, E. G. Cooch, and M. J. Conroy.) pp. 255–269. (Springer: New York, NY, USA.)
- Fajardo, U., Cossíos, D., and Pacheco, V. (2014). Dieta de *Leopardus colocolo* (Carnívora: Felidae) en la Reserva Nacional de Junín, Junín, Perú. *Revista Peruana de Biología* **21**, 61–70. doi:10.15381/rpb.v21i1.8248
- Foster, V. C., Sarmiento, P., Sollmann, R., Tôrres, N., Jácomo, A. T., Negrões, N., Fonseca, C., and Silveira, L. (2013). Jaguar and puma activity patterns and predator–prey interactions in four Brazilian biomes. *Biotropica* **45**, 373–379. doi:10.1111/btp.12021
- Gardner, B., Reppucci, J., Lucherini, M., and Royle, J. A. (2010). Spatially explicit inference for open populations: estimating demographic parameters from camera-trap studies. *Ecology* **91**, 3376–3383. doi:10.1890/09-0804.1

- Gobierno Autónomo Municipal de Calacoto (2008). 'Plan de Desarrollo Municipal, Municipio de Calacoto 2008–2012.' (Gobierno Autónomo Municipal de Calacoto: La Paz, Bolivia.)
- Haines, A. M., Grassman, L. I., Jr, and Tewes, M. E. (2004). Survival of radiocollared adult leopard cats *Prionailurus bengalensis* in Thailand. *Acta Theriologica* **49**, 349–356. doi:10.1007/BF03192533
- Huaranca, J. C., and Villalba, M. L. (2011). 'Opciones para el Establecimiento de la Estación de Investigación IE-AGA. Conservation of Andean Cat in Ciudad de Piedra Area.' (Alianza Gato Andino: La Paz, Bolivia.)
- Huaranca, J. C., Pacheco, L. F., Villalba, L., and Torrez, A. R. (2013). Ciudad de Piedra, an important site for the conservation of Andean cats in Bolivia. *Cat News* **58**, 1–8.
- Ivan, J. S., White, G. C., and Shenk, T. M. (2013). Using simulation to compare methods for estimating density from capture–recapture data. *Ecology* **94**, 817–826. doi:10.1890/12-0102.1
- Jiménez, J. E., Yáñez, J. L., Tabilo, E. L., and Jaksic, F. M. (1996). Niche-complementarity of South American foxes: reanalysis and test of a hypothesis. *Revista Chilena de Historia Natural* **69**, 113–123.
- Jones, M., and Dayan, T. (2000). Foraging behavior and microhabitat use by spiny mice, *Acomys cahirinus* and *A. russatus*, in the presence of Blanford's fox (*Vulpes cana*) odor. *Journal of Chemical Ecology* **26**, 455–469. doi:10.1023/A:1005417707588
- Kelt, D. A., and Van Vuren, D. H. (2001). The ecology and macroecology of mammalian home range area. *American Naturalist* **157**, 637–645. doi:10.1086/320621
- Kolowski, J. M., and Woolf, A. (2002). Microhabitat use by bobcats in southern Illinois. *The Journal of Wildlife Management* **66**, 822–832. doi:10.2307/3803146
- Linkie, M., and Ridout, M. S. (2011). Assessing tiger–prey interactions in Sumatran rainforests: tiger–prey temporal interactions. *Journal of Zoology* **284**, 224–229. doi:10.1111/j.1469-7998.2011.00801.x
- López, G., López-Parra, M., Garrote, G., Fernández, L., del Rey-Wamba, T., Arenas-Rojas, R., García-Tardío, M., Ruiz, G., Zorrilla, I., Moral, M., and Simón, M. A. (2014). Evaluating mortality rates and causalities in a critically endangered felid across its whole distribution range. *European Journal of Wildlife Research* **60**, 359–366. doi:10.1007/s10344-013-0794-8
- Lucherini, M., Luengos Vidal, E., and Merino, M. J. (2008). How rare is the rare Andean cat? *mammalia* **72**, 95–101. doi:10.1515/MAMM.2008.018
- Lucherini, M., Reppucci, J. I., Walker, R. S., Villalba, M. L., Wursten, A., Gallardo, G., Iriarte, A., Villalobos, R., and Perovic, P. (2009). Activity pattern segregation of carnivores in the high Andes. *Journal of Mammalogy* **90**, 1404–1409. doi:10.1644/09-MAMM-A-002R.1
- Lucherini, M., Eizirik, E., de Oliveira, T. G., Pereira, J., and Williams, R. (2016). *Leopardus colocolo*. In 'The IUCN Red List of Threatened Species 2016: e.T15309A97204446'. Available at <http://www.iucnredlist.org/details/15309/0> [verified 12 May 2017].
- Macdonald, D. W., and Loveridge, A. J. (Eds) (2010). 'Biology and Conservation of Wild Felids.' (Oxford University Press: Oxford, UK.)
- Marino, J., Lucherini, M., Villalba, M. L., Bennett, M., Cossíos, D. E., Iriarte, A., Perovic, P., and Sillero-Zubiri, C. (2010). Highland cats: ecology and conservation of the rare and elusive Andean cat. In 'Biology and Conservation of Wild Felids'. (Eds D. W. Macdonald and A. J. Loveridge.) pp. 581–596. (Oxford University Press: Oxford, UK.)
- Marino, J., Bennett, M., Cossíos, D., Iriarte, A., Lucherini, M., Plissock, P., Sillero-Zubiri, C., Villalba, L., and Walker, S. (2011). Bioclimatic constraints to Andean cat distribution: a modelling application for rare species: bioclimatic constraints to Andean cat distribution. *Diversity & Distributions* **17**, 311–322. doi:10.1111/j.1472-4642.2011.00744.x
- McNab, B. K. (1963). Bioenergetics and the determination of home range size. *American Naturalist* **97**, 133–140. doi:10.1086/282264
- Napolitano, C., Bennett, M., Johnson, W. E., O'Brien, S. J., Marquet, P. A., Barria, I., Poulin, E., and Iriarte, A. (2008). Ecological and biogeographical inferences on two sympatric and enigmatic Andean cat species using genetic identification of faecal samples. *Molecular Ecology* **17**, 678–690. doi:10.1111/j.1365-294X.2007.03606.x
- Noss, A. J., Gardner, B., Maffei, L., Cuéllar, E., Montaña, R., Romero-Muñoz, A., Sollman, R., and O'Connell, A. F. (2012). Comparison of density estimation methods for mammal populations with camera traps in the Kaa-Iya del Gran Chaco landscape: density estimation with camera traps in the Chaco. *Animal Conservation* **15**, 527–535. doi:10.1111/j.1469-1795.2012.00545.x
- Nowell, K., and Jackson, P. (1996). 'Wild Cats: Status Survey and Conservation Action Plan'. (Gland: IUCN.) Available at http://www.catsg.org/fileadmin/filesharing/4.Library/4.1_Cat_Library/cat-action-plan-info-form.pdf [verified 5 May 2019].
- Pereira, L. J. A. (2009). Efectos del manejo ganadero y disturbios asociados sobre la ecología trófica y espacial y la demografía del gato montés (*Leopardus geoffroyi*) en el desierto del monte, Argentina. Ph.D. Thesis, Universidad de Buenos Aires, Argentina.
- R Core Team (2016). 'R: a Language and Environment for Statistical Computing.' (R Foundation for Statistical Computing: Vienna, Austria.) Available at <https://www.R-project.org/> [verified 6 May 2016].
- Reppucci, J., Gardner, B., and Lucherini, M. (2011). Estimating detection and density of the Andean cat in the high Andes. *Journal of Mammalogy* **92**, 140–147. doi:10.1644/10-MAMM-A-053.1
- 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
- Riley, S. P. D. (2006). Spatial ecology of bobcats and gray foxes in urban and rural zones of a national park. *The Journal of Wildlife Management* **70**, 1425–1435. doi:10.2193/0022-541X(2006)70[1425:SEOBAG]2.0.CO;2
- Ross, J., Hearn, A. J., Johnson, P. J., and Macdonald, D. W. (2013). Activity patterns and temporal avoidance by prey in response to Sunda clouded leopard predation risk: activity of Sunda clouded leopards and their prey. *Journal of Zoology* **290**, 96–106. doi:10.1111/jzo.12018
- Royle, J. A., and Gardner, B. (2011). Hierarchical spatial capture–recapture models for estimating density from trapping arrays. In 'Camera Traps in Animal Ecology: Methods and Analyses'. (Eds A. F. O'Connell, J. D. Nichols, and K. U. Karanth.) pp. 163–190. (Springer: New York, NY, USA.)
- 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
- Santini, L., Isaac, N. J. B., Maiorano, L., Ficetola, G. F., Huijbregts, M. A. J., Carbone, C., and Thuiller, W. (2018). Global drivers of population density in terrestrial vertebrates. *Global Ecology and Biogeography* **27**, 968–979. doi:10.1111/geb.12758
- Santos, F., Carbone, C., Wearn, O. R., Rowcliffe, J. M., Espinosa, S., Lima, M. G. M., Ahumada, J. A., Gonçalves, A. L. S., Trevelin, L. C., Alvarez-Loayza, P., Spironello, W. R., Jansen, P. A., Juen, L., and Peres, C. A. (2019). Prey availability and temporal partitioning modulate felid coexistence in Neotropical forests. *PLoS One* **14**, e0213671. doi:10.1371/journal.pone.0213671
- Schoener, T. W. (1974). Resource partitioning in ecological communities. *Science* **185**, 27–39. doi:10.1126/science.185.4145.27
- Silva, M., Brimacombe, M., and Downing, J. A. (2001). Effects of body mass, climate, geography, and census area on population density of terrestrial mammals. *Global Ecology and Biogeography* **10**, 469–485. doi:10.1046/j.1466-822x.2001.00261.x
- Sollmann, R., Gardner, B., and Belant, J. L. (2012). How does spatial study design influence density estimates from spatial capture–recapture models? *PLoS One* **7**, e34575. doi:10.1371/journal.pone.0034575
- Suraci, J. P., Clinchy, M., and Zanette, L. Y. (2017). Do large carnivores and mesocarnivores have redundant impacts on intertidal prey? *PLoS One* **12**, e0170255. doi:10.1371/journal.pone.0170255

- Tarifa, T., and Yensen, E. (2001). Mammals of Bolivian *Polylepis* woodlands. *Revista Boliviana de Ecología* **9**, 29–44.
- Tellaache, C. G. (2015). Ecología y uso del espacio de dos especies de félidos, Gato Andino (*Leopardus jacobita*) y Gato del Pajonal (*L. colocolo*) en la región Altoandina, Prov. de Jujuy. Ph.D. Thesis, Universidad Nacional del Sur, Bahía Blanca, Argentina.
- Teran, J., and Huaranca, J. C. (2012). 'Evaluación de la Vegetación del Área de Ciudad de Piedra, La Paz-Bolivia. Conservation of Andean Cat in Ciudad de Piedra Area.' (Andean Cat Alliance: La Paz, Bolivia.)
- Theuerkauf, J., Jedrzejewski, W., Schmidt, K., Okarma, H., Ruczynski, I., Snieszko, S., and Gula, R. (2003b). Daily patterns and duration of wolf activity in the Bialowieza Forest, Poland. *Journal of Mammalogy* **84**, 243–253. doi:10.1644/1545-1542(2003)084<0243:DPADOW>2.0.CO;2
- Torrico, J. O. (2009). Distribución, abundancia relativa de rastros y dieta de carnívoros alto andinos en dos zonas de la Reserva Eduardo Avaroa, Potosí-Bolivia. B.Sc. Thesis, Universidad Mayor de San Andrés, La Paz, Bolivia.
- Villalba, M. L., Alfaro, F. D., Huaranca, J. C., and Gallardo, G. (2009a). *Leopardus jacobita*. In 'Libro Rojo de la Fauna Silvestre de Vertebrados de Bolivia'. pp. 451–453. (Ministerio de Medio Ambiente y Agua: La Paz, Bolivia.)
- Villalba, M. L., Delgado, E., and Berna, M. (2009b). Activity patterns and home range of Andean cat and Pampas cat in southern Bolivia. In '10th International Mammalogical Congress Abstracts'. (Eds. E. Nevo, M. Mares, C. Johnson, G. Marroig, and P. Marquet). p. 187. (Mendoza, Argentina.)
- Villalba, M. L., Gallardo, G., and Huaranca, J. C. (2009c). *Leopardus colocolo*. In 'Libro Rojo de la Fauna Silvestre de Vertebrados de Bolivia'. pp. 525–527. (Ministerio de Medio Ambiente y Agua: La Paz, Bolivia.)
- Villalba, M. L., Huaranca, J. C., Gallardo, G., Viscarra, M. E., Torrico, J. O., and Bernal, N. (2009d). Distribution and diet of sympatric wildcats *Leopardus jacobita* and *L. colocolo*, in the Andes at Bolivia. In '10th International Mammalogical Congress Abstracts'. (Eds. E. Nevo, M. Mares, C. Johnson, G. Marroig, and P. Marquet). p. 113. (Mendoza, Argentina.)
- Villalba, L., Lucherini, M., Walker, R. S., Lagos, N., Cossíos, D., Bennett, M., and Huaranca, J. C. (2016). *Leopardus jacobita*. In 'The IUCN Red List of Threatened Species 2016: e.T15452A50657407'. Available at <http://www.iucnredlist.org/details/15452/0> [verified 12 May 2017].
- Viscarra, M. E. (2008). Distribución, densidad y dieta de carnívoros en cuatro tipos de hábitat en un área de la Provincia Sud Lipez (Potosí-Bolivia). B.Sc. Thesis, Universidad Mayor de San Andrés, La Paz, Bolivia.
- Walker, R. S., Novaro, A. J., Perovic, P., Palacios, R., Donadio, E., Lucherini, M., Pia, M., and López, M. S. (2007). Diets of three species of Andean carnivores in high-altitude deserts of Argentina. *Journal of Mammalogy* **88**, 519–525. doi:10.1644/06-MAMM-A-172R.1
- Yensen, E., and Seymour, K. L. (2000). *Oreailurus jacobita*. *Mammalian Species* No. **644**, 1–6. doi:10.1644/1545-1410(2000)644<0001:OJ>2.0.CO;2
- Zanón-Martínez, J. I., Kelly, M. J., Mesa-Cruz, J. B., Sarasola, J. H., Dehart, C., and Travaini, A. (2016). Density and activity patterns of pumas in hunted and non-hunted areas in central Argentina. *Wildlife Research* **43**, 449–460. doi:10.1071/WR16056