Habitat use and activity patterns of *Puma concolor* in a human-dominated landscape of central Argentina

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Habitat loss, poaching, and legal hunting are the main causes of decline in populations of pumas (*Puma concolor*) globally. We used camera trapping to assess the habitat use and daily activity patterns of pumas, and we identified the major factors affecting this species, in a human-dominated landscape in central Argentina. The intensity of habitat use by pumas was related positively to the presence of woodland, habitat complexity, and richness of wild prey. Pumas also avoided areas with a high concentration of ranches, indicators of more-intense human activity. Although some seasonal variation was detected in the activity patterns, pumas clearly preferred nighttime hours. We conclude that human-related factors strongly affect habitat use and activity of pumas in central Argentina's rangelands.

La pérdida de hábitat y la caza ilegal y legal son las principales causas de la disminución de las poblaciones de puma a lo largo de su distribución. Aún cuando este felino se caracteriza por una gran plasticidad ecológica, los factores que afectan su supervivencia en áreas altamente modificadas por el hombre son poco conocidos. En este trabajo, se utilizó el trampeo fotográfico para determinar el uso de hábitat, el patrón de actividad del puma y los factores que pueden afectar a esta especie en un paisaje dominado por las actividades antrópicas en el centro de Argentina. La intensidad del uso del hábitat de los pumas fue favorecida por la presencia de bosque semi-cerrado, la complejidad de hábitat y la riqueza de presas silvestres. Además, los pumas evitaron las áreas con una elevada densidad de propiedades, la cual fue considerada como un indicador de una mayor actividad humana. Si bien se identificaron variaciones estacionales en el patrón de actividad, los pumas prefirieron claramente las horas nocturnas. Concluimos que los factores antrópicos parecen afectar fuertemente el uso del hábitat y los patrones de actividad del puma en un área ganadera del centro de Argentina.

Key words: Carnivora, camera trapping, Felidae, Generalized Linear Mixed Models, habitat preferences, human–wildlife conflict, mountain lion, prey richness

Puma concolor has an extensive geographic distribution and is characterized by wide ecological plasticity (Nowell and Jackson 1996). However, its abundance is thought to be declining globally (Nielsen et al. 2015), primarily due to anthropogenic pressure (Logan and Sweanor 2001; Murphy and Macdonald 2010; De Angelo et al. 2011). Anthropic factors (e.g., agricultural and livestock activities, roads, and inhabited areas) and variables such as vegetation cover, topography, slope, elevation, and presence of water bodies can affect the occurrence of this felid directly and through effects on its prey (e.g., Holmes and Laundré 2006; Sweanor et al. 2008; Monroy-Vilchis et al. 2009). Across its distribution, the puma is found

from high mountains to deserts (Nowell and Jackson 1996), including landscapes dominated by human activities (Sweanor et al. 2008; Zarco-González et al. 2013; Caruso et al. 2016).

Humans represent the main threat to several species of carnivores (Theuerkauf 2009). Recent studies have shown that human-induced fear can stimulate behavioral adjustments in pumas, which then avoid encountering humans (Smith et al. 2015, 2017). Thus, in landscapes dominated by human activities, modifications in the habitat use and activity patterns of this felid are expected. Although information on the ecology of pumas in these types of landscapes is limited (Mazzolli 2000; Scognamillo et al. 2003), in anthropogenically modified areas,

pumas tend to occur in topographically heterogeneous environments with abundant vegetation cover (Riley and Malecki 2001; Silveira 2004), high abundance of wild prey (e.g., ungulates—Riley and Malecki 2001), and far from paved roads (Dickson et al. 2005; Caruso et al. 2015). Whereas pumas are mainly nocturnal and crepuscular (Beier et al. 1995; Paviolo et al. 2009; Gutiérrez-González and López-González 2017), they concentrate their movements during the night in unprotected areas with intense human activity (Van Dyke et al. 1986; Sweanor et al. 2008; Zanón-Martínez et al. 2016).

Across their distribution, pumas are persecuted and hunted as a preventive measure and in retaliation for predation on livestock (Mazzolli et al. 2002; Inskip and Zimmermann 2009). In the southern part of the Argentine Espinal (325,360 km²), pumas are heavily persecuted by humans due to livestock predation (Guerisoli et al. 2017), and their distribution is limited by modifications of natural habitats (Caruso et al. 2015). From the late nineteenth century to 1955, the Espinal ecoregion has been affected by severe landscape transformations (Matteucci 2012) primarily associated with the expansion of farming and ranching activities (Arturi 2005). Currently, only 0.6% of this ecoregion is under protection (total protected area: 1,690 km²; Ministry of Environment and Sustainable Development 2010) and over 40% of the natural habitats have been converted into croplands and rangelands (Arturi 2005; Brown et al. 2005). A landscape-scale study in the southern Espinal found that pumas prefer areas with a greater proportion of semi-open natural habitat far from roads and urban settlements (Caruso et al. 2016). However, it remains unclear how habitat composition and structure at a local scale influence habitat use by this species. We assessed at a local spatial scale what factors enable pumas to live in the combination of bushlands, grasslands, and croplands that typically shapes the rangelands of the southern Espinal today. We expected that in addition to habitat type, the availability of prey, disturbance by humans, and habitat complexity could affect the occurrence of pumas locally. Specifically, we tested the following predictions: 1) The intensity of habitat use by pumas in the southern Espinal is positively affected by the presence of a complex mix of closed and semi-open habitats, where vegetation configuration provides pumas with shelter from humans as well as improved accessibility to prey (Holmes and Laundré 2006; Laundré 2010; Caruso et al. 2015). 2) The richness of wild prey favors puma presence. In spite of the abundance of livestock, wild prey is still important in the diet of this felid in this region (M. Guerisoli, pers. obs.). Thus, we assumed that availability of wild prey would affect habitat use by pumas. Unfortunately, because our camera traps were specifically set up to maximize puma detection, we expected that they would not provide reliable information on prey abundance and assess the effect of prey richness instead. 3) Pumas avoid areas where anthropogenic activity is intense, and times of the day when humans are more active and thus concentrate their activity in the nocturnal and crepuscular hours (Van Dyke et al. 1986; Paviolo et al. 2009). Given the negative effect of the distance to roads and to urban areas on the presence of pumas at a landscape scale (Caruso et al. 2016), we

hypothesized that at a more-reduced spatial scale, these felids would minimize the chances of contact with humans.

Materials and Methods

Study area.—The study area comprised three contiguous rangeland sites in the southernmost part of Buenos Aires province within the Argentine Espinal (Fig. 1). This ecoregion is characterized by xerophytic deciduous woodlands, prairies dominated by grasslands, and prairies intermixed with extensive scrublands (Fernández and Busso 1999). The climate is temperate. The average annual temperature is 15°C (Menéndez and La Rocca 2007), but seasonal variations are pronounced, and daytime temperatures can reach 44°C, frequently exceeding 35°C in the summer months (Kloster and Ernst 2016). The total annual rainfall is between 200 and 700 mm with significant water deficit during the dry summer season (Brown et al. 2005; Menéndez and La Rocca 2007).

Sampling design.—Data were collected in 2014, 2015, and 2016 through three camera-trapping sessions (Fig. 1). Eighty-six camera-trap stations were distributed in the study area proportionally to the area occupied by the main habitats (cropland, grassland, grassland with shrubs, and bushland), based on a digital land cover map (1:250,000). We used heat and motion, infrared-triggered cameras (Reconyx, Inc., Holmen, Wisconsin; ScoutGuard, Boly Media Communications, Inc., Santa Clara, California; Moultrie Feeders, Birmingham, Alabama; Bushnell Corporation, Overland Park, Kansas) set to take pictures 24 h/day with a 1-min delay between exposures. In 2014, 2015, and 2016, we installed 28, 25, and 33 cameras, respectively.

In each area, all cameras were activated simultaneously. The area surveyed in 2014 (January to December) was located approximately 50 km from a national highway and was characterized mainly by bushlands and grasslands with shrubs. This area had the lowest degree of anthropic disturbance. The second area, surveyed in 2015 (January to December), was dominated by croplands and was close to the national highway. Grassland was the main habitat in the area sampled in 2016 (May to December), which was also relatively close to the national highway (Fig. 1). Camera-trap stations were deployed, on average, 5 km apart from each other to reduce spatial autocorrelation and cover a significant area for the species in each session, considering an average puma home range size of 24–363 km² (Franklin et al. 1999; Dickson and Beier 2002; Laundré and Loxterman 2007; Elbroch and Wittmer 2012). Sampling stations were baited with odoriferous bait (Bobcat Urine or Bob Gland Lure, Stanley Hawbaker and Sons Lures, Fort Loudon, Pennsylvania) and checked at least once per month. Sampling effort is the sum of the number of effective days (excluding those days when cameras did not work) for each station. All puma events were classified according to the date, time, and season (winter or summer). Since few events were obtained during spring and autumn, and the trapping sessions were concentrated mainly in winter and summer, we considered only these two seasons, which we defined in relation to the equinoxes.
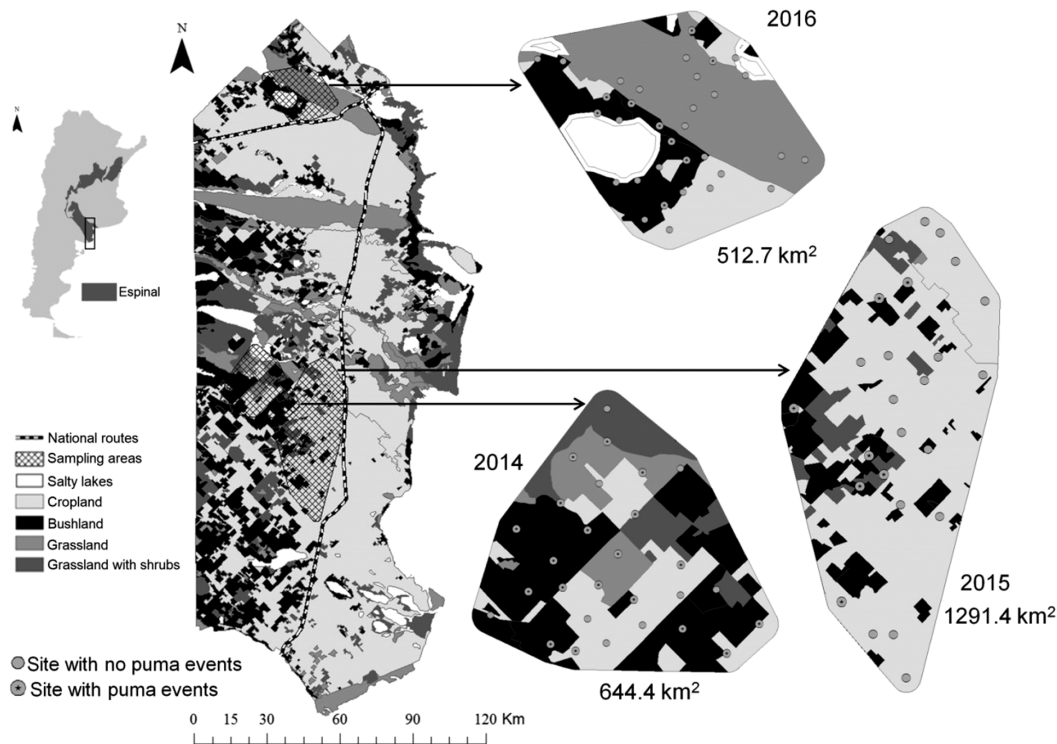
Fig. 1.—Study area: three camera-trap sampling sites, details of the main habitats, and major landscape features.

Habitat use: predictive variables.—On a vector map provided by the National Institute of Agriculture Technology (EEA Hilario Ascasubi), we drew a 2-km buffer around each sampling station (an area of 12.57 km^2), in order to characterize the sites according to vegetation type, anthropic disturbance, richness of wild prey, and structural complexity of the habitat. This radius was determined to maximize the size of buffer areas while minimizing overlap between camera sites.

Inside the buffer area, we calculated the proportions of the main habitat types: bushland (comprising closed bushland and the more open grassland with shrubs), cropland, and grassland.

To estimate prey richness, we registered the presence of potential prey species obtained through the same camera-trap sampling. The species considered as prey were guanaco (*Lama guanicoe*), wild boar (*Sus scrofa*), Patagonian mara (*Dolichotis patagonum*), plains vizcacha (*Lagostomus maximus*), European hare (*Lepus europaeus*), armadillos (large hairy armadillo [*Chaetophractus villosus*], screaming hairy armadillo [*C. vellerosus*], and pichi [*Zaedyus pichiy*]), common rhea (*Rhea americana*), and partridges (elegant crested tinamou [*Eudromia elegans*], spotted nothura [*Nothura maculosa*], Darwin's nothura [*Nothura darwinii*], and brushland tinamou [*Nothoprocta cinerascens*]). Because sampling effort varied across sampling sites, the number of prey species per site was divided by the sampling effort at each site to obtain a wild prey richness index.

To characterize the structural complexity of the habitat within the buffer areas, we used four metrics that reflect the distribution and abundance of habitat patches: the Shannon's Evenness Index (SEI—Shannon and Weaver 1949; Pielou 1966), Mean Shape Index (MSI—McGarigal et al. 1994; Daye and Healey 2015), Edge Density (ED—Daye and Healey 2015), and Total

Edge Perimeter of Patches (TE). We used the Patch Analyst tool of ArcGis 10.1 (ESRI 2012) to calculate these metrics.

We measured three metrics related to anthropogenic disturbance. We georeferenced all the inhabited houses within the study area and calculated the minimum distance to the nearest house (Dhouse) for each camera-trap site. Additionally, we computed the number of properties within the buffer of each camera station and divided it by the size of the buffer area (Propd) and the minimum distance to the nearest road (Droad). The variables included in the model are summarized in Table 1.

Habitat use: statistical analyses.—We performed a Kendall correlation analysis (Kendall 1938) to eliminate highly correlated variables and reduce the multicollinearity among predictors (Zuur et al. 2009). Our initial set of variables included: Crop (proportion of cropland), Grass (proportion of grassland), Bush (proportion of grassland with shrubs and bushland), Droad, Dhouse, Propd, Rich (richness of wild prey), ED, MSI, TE, and SEI. Because the correlation matrix showed the existence of a group of highly correlated and ecologically related variables, we performed a principal components analysis (PCA) and used the loadings of the first component as a new predictor representing the linear combination of the original correlated variables (Hotelling 1933; Legendre and Legendre 2012).

Finally, we fit a set of binomial Generalized Linear Mixed Models (GLMMs—Zuur et al. 2009) using the intensity of use (defined as the sum of the independent puma events obtained) per sampling site as the dependent variable. We considered as independent all the consecutive photographs of pumas taken more than 30 min apart. The GLMMs were performed by adjusting a negative binomial distribution, setting sampling effort as the exposure variable (offset) and "year" as an intercept

random effect. Before applying the analyses, all the data were scaled, with the exception of the first component of the PCA since it was a linear combination of scaled data. Using the function "dredge" of the package MuMIn in R (R Core Team 2017), we created a list of all possible models given the list of predictors and assuming only additive effects. We ranked all models using the Akaike information criterion adjusted for small samples (AICc) and used the ΔAICc and the AICc weights to evaluate the relative importance of each model within the final set of models (Burnham and Anderson 2002). We used a multimodel inference approach (Burnham and Anderson 2002) and averaged the set of models with ΔAICc < 2. The regression coefficients (β) in the averaged model were considered to have a significant effect when the corresponding 95% confidence intervals (CI) excluded zero (Zeller et al. 2011).

Activity patterns.—To characterize activity patterns of pumas, we used the independent events obtained through the three camera-trapping surveys and by additional camera traps placed to monitor two areas where live-capture sessions for pumas were carried out in 2015 and 2016. To provide a general description of puma activity, we pooled the data from all study sites and divided the photos obtained into four time periods: day, night, dawn (from 1 h before to 1 h after the mean sunrise hour for the study period), and dusk (from 1 h before to 1 h after the mean sunset hour for the study period—Theuerkauf et al. 2003; Farris et al. 2015).

Activity patterns: statistical analyses.—We used Fisher's exact test (Fisher 1922) to test if puma events were distributed homogeneously across the segments of the day (dawn, day, dusk, and night) and applied Jacobs' selection index (Jacobs 1974) to identify possible preferences for a given segment. To graphically describe the activity pattern of pumas, detect hourly peaks, and estimate overlap between seasons, we used a kernel density analysis (Ridout and Linkie 2009; Oliveira-Santos et al. 2013). To compare activity patterns between seasons, we calculated the coefficient of overlap (Δ *Dath*), which varies from 0 (no overlap) to 1 (complete overlap—Ridout and Linkie 2009; Meredith and Ridout 2016). Specifically, we used the Δ *Dath4* coefficient because it is the most appropriate estimator for samples with $n > 75$ (Meredith and Ridout 2016). We calculated the 95% confidence intervals for the overlap coefficient from 500 bootstrap samples. These analyses were carried out with the circular and overlap packages of R (R Core Team 2017).

RESULTS

Habitat use.—Our 86 camera-trap sites covered an area of 1,787 km^2 (buffer areas excluded), totaled a sampling effort of 10,621 camera-trap days (mean ± *SD* sampling effort per station: 123.5 ± 76.7 trap days), and collected 105 puma events (1.2 ± 2.2 events per site) in 41% of the sampling sites (Fig. 1). The mean (± *SD*) number of species per site was 2.3 (± 2.04).

Following the results of the correlation matrix (Supplementary Data SD1), we carried out a PCA with the four variables that were significantly correlated (MSI, TE, ED, and SEI) to create a new single variable that would characterize the structural complexity of habitat (Hc) in the buffers. The four variables were strongly and positively associated with the first component and the proportion of variability explained by this component (PC1) was 0.9 (Supplementary Data SD2).

Four models formed the set with ΔAICc < 2 (Table 2). Only the variables Bush, Hc, and Dprop were included in the

Table 1.—Variables used to explain the intensity of habitat use by pumas (*Puma concolor*) with the origin of the data and variable range.

Variable	Data origin	Variable range
Proportion of habitat type (Crop, Grass, Bush)	Habitat vector map	0–100%
Prey richness index (Rich)	Camera trap records (species count)	0–0.18
Shannon's Evenness Index (SEI)	Vector map	0–1
Mean Shape Index (MSI)	Vector map	0–2.06
Edge Density (ED)	Vector map	0–35 (m^2)
Total Edge Perimeter of Patches (TE)	Vector map	0–44 (m)
Distance to the nearest house (Dhouse)	Georeferenced houses	300–11,889 (m)
Density of ranches (Propd)	Cadastral map	0.07–1.51 (ranches/km^2)
Distance to the nearest road (Droad)	Road map	0.1–9,149 (m)

Table 2.—Parameters of the Generalized Linear Mixed Models (GLMMs) of habitat use by pumas (i.e., number of puma events per site) in rangelands of central Argentina. Only parameters for the set of models with ΔAICc < 2 are reported. Int = intersection; *d.f.* = degrees of freedom; LogLik = log likelihood function; ΔAICc = difference in value of Akaike's information criterion between the focal model and the top-ranked model; Est. = estimator for the GLMM average model; *CI* = 2.5 and 97.5 confidence intervals of the average model. Variables are described in Table 1 and "Materials and Methods."

#	Int.	Crop	Droad	Dhouse	Grass	Bush	Hc	Dprop	Rich	df	LogLik	ΔAICc	Weight
1	−5.8	-	-	-	-	0.35	0.79	−1.82	0.48	7	−94.4	0	0.1
2	−5.9	-	-	0.35	-	0.37	0.91	−1.85	0.51	8	−93.2	0.04	0.1
3	−5.8	-	-	-	-	0.28	0.81	−2	-	6	−96.5	1.8	0.4
4	−6	0.2	-	0.37	-	0.45	0.95	−1.96	0.51	9	−92.9	1.9	0.4
Est	-	0.2	-	0.35	-	0.36	0.85	−1.87	0.49				
CI (2.5%)	−6.5	−0.3	-	−0.09	-	0.03	0.4	−2.7	0.05				
CI (97.5%)	−5.2	0.7	-	0.8	-	0.6	1.3	0.8	0.9				

four models (Table 2). The averaged model and the confidence intervals (Table 2) suggested that puma occurrence was affected by two variables related to the composition of the landscape (Bush) and habitat complexity (Hc): one variable related to the presence of wild prey (Rich) and one variable of anthropic disturbance (Dprop; Supplementary Data SD3; Table 2). The latter was the only variable with a negative effect (Table 2).

Activity patterns.—We obtained 129 records of puma activity. The events were not homogeneously distributed ($P < 0.05$), but rather concentrated primarily in the night, and secondarily during the twilight hours (Table 3). Jacobs' selection index values showed that pumas strongly selected the night and avoided the day (Table 3).

Winter.—During winter ($n = 56$ events), the number of events per hour was greatest at night and dawn (Table 3). Jacobs' selection index indicated a positive preference of pumas towards the nocturnal phase and avoidance of day and dusk, while pumas did not show either a strong positive or negative tendency toward dawn (Table 3). Activity showed a first peak after sunset, between 1900 and 2200 h, and then two less-pronounced peaks between 0000 and 0800 h (Fig. 2).

Summer.—In summer ($n = 73$ events), the difference in the number of events per hour between day and night was slightly smaller than in winter (Table 3). Jacobs' selection index showed a very strong preference for the night and a negative value for the day. Sunset had a slightly positive selection value (Table 3). The kernel density curve showed two nocturnal activity peaks in the summer: a first peak, very marked, after sunset, and a second, less-pronounced peak between 0300 and 0500 h (Fig. 2).

The overlap between activity patterns in summer and winter was 0.66 ($CI = 0.5$–0.76). Both seasonal curves showed similarly steep slopes marking the start of activity after sunset, suggesting that the dissimilarity between them was primarily related to the seasonal shifting of sunset and sunrise. However, the curves differed in the concentration of activity during nighttime, which was much greater in summer (Fig. 2).

DISCUSSION

In agreement with our predictions, pumas in the anthropogenically modified landscape of central Argentina used more intensively areas with a greater number of prey species and where habitat was characterized by the presence of bushland and greater structural complexity (Fig. 3). Bushland was the habitat with the most abundant vegetation cover in the study area, so its use by pumas is consistent with results from other areas (Silveira 2004; Dickson et al. 2005). The presence of semiclosed habitat or the combination of dense vegetation in proximity to open areas can positively influence the effectiveness of the predation strategy of pumas, providing a balance between the abundance of prey and its "catchability" (Scognamillo et al. 2003; Holmes and Laundré 2006). In the southern Espinal, puma prey is more
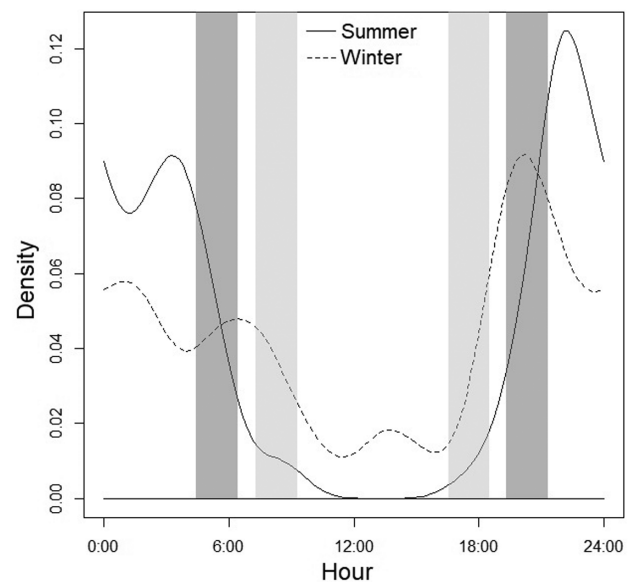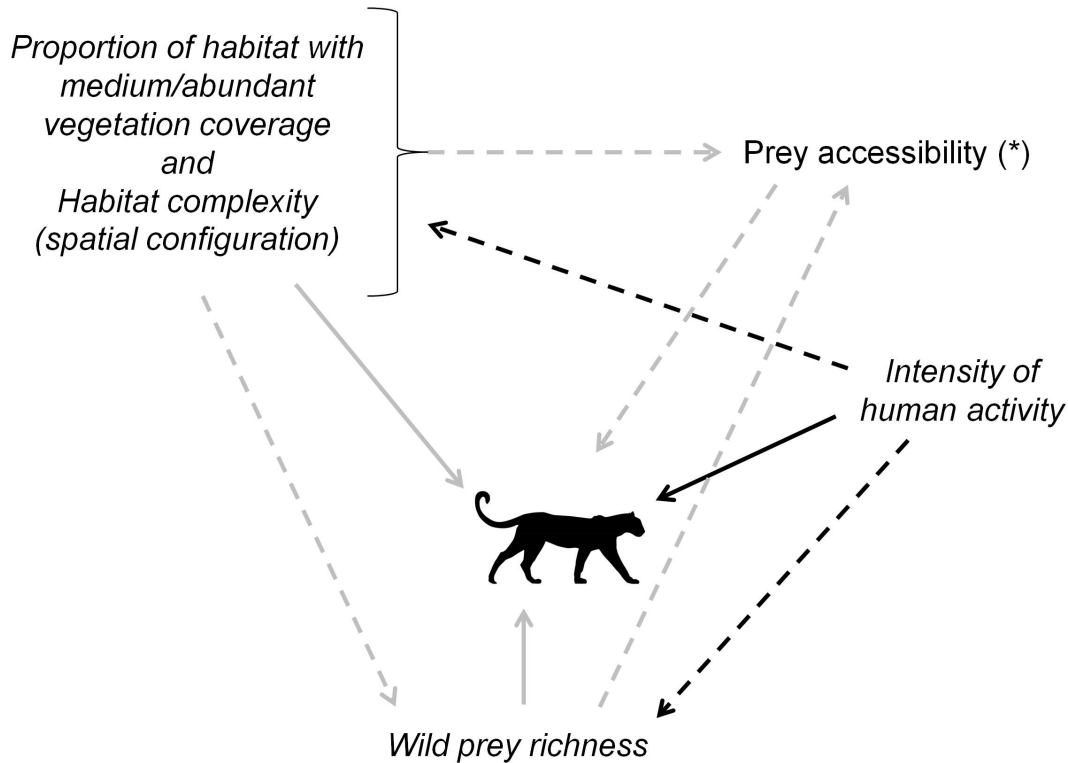

Fig. 2.—Activity pattern of pumas (*Puma concolor*) in summer and winter in rangelands of central Argentina (kernel density analysis): density of activity events by hour of the day. The light gray and dark gray stripes show twilight in winter and summer, respectively.

Table 3.—Activity patterns of puma (*Puma concolor*) in rangelands of central Argentina, according to the four segments of the day overall, and separated by winter and summer season. Jacobs' selection index may vary between −1, indicative of strong avoidance, and 1, indicative of strong preference.

Overall	Dawn	Day	Dusk	Night
Proportion of events (%)	8.5 ($n = 11$)	7.8 ($n = 10$)	8.5 ($n = 11$)	75.1 ($n = 97$)
Frequency (events per hour)	5.5	1.01	5.5	9.9
Jacobs' selection index	0.003	−0.79	0.003	0.62

Winter	Dawn	Day	Dusk	Night
Proportion of events	8.9 ($n = 5$)	8.9 ($n = 5$)	5.4 ($n = 3$)	76.8 ($n = 43$)
Frequency	2.5	0.6	1.5	3.5
Jacobs' selection index	0.02	−0.63	−0.2	0.5

Summer	Dawn	Day	Dusk	Night
Proportion of events	8.2 ($n = 6$)	6.8 ($n = 5$)	11 ($n = 8$)	74 ($n = 54$)
Frequency	3	0.4	4	7.6
Jacobs' selection index	−0.01	−0.87	0.14	0.73

(*) Prey accessibility is proposed as a possible connection between the two variables of habitat composition and habitat complexity and the puma.

Fig. 3.—Schematic interpretation of the relationships among the variables that affect habitat use of pumas (*Puma concolor*) in rangelands of central Argentina. The variables considered in the model are in italics. The gray arrows indicate a positive effect and the black arrows a negative effect. The solid arrows show the connections identified by our GLMM model, and dashed arrows indicate a hypothetical relationship.

abundant in open areas (Olla 2016). However, pumas are stealth predators (e.g., Hornocker 1970; Logan and Sweanor 2001) and the success of their hunting strategy is maximized in habitats that offer cover for concealment and stalking, and, at the same time, open spaces to pursue and capture prey (Laundré 2010). Accordingly, other studies found that the intersection between open and closed environments increased prey availability, both in terms of diversity (Polisar 2000; Scognamillo et al. 2003, for the Venezuelan Llanos) and catchability (Laundré and Hernández 2003; Laundré 2010, for the montane forests of Idaho and Utah). Thus, it is possible that the preference of pumas for sites with greater habitat complexity in our study area is also related to prey richness, as both factors would affect the accessibility of wild prey.

In central Argentina, *P. concolor* is hunted in response to predation on sheep and calves or to prevent attacks on livestock (Zanón-Martínez et al. 2016; Guerisoli et al. 2017). For this reason, the positive relationship between the richness of wild prey and puma occurrence has implications for puma conservation. We did not assess the effect of livestock on habitat use by pumas because the relatively intense management by ranchers caused frequent spatial and temporal variations in the presence and abundance of these animals and made the estimation of livestock abundance difficult. Although livestock is an alternative source of food, the areas preferred by pumas had a higher number of wild prey species. Consistently, preliminary results

indicate that wild prey is important in the diet of pumas in our study area (M. Guerisoli, pers. obs.). In concordance with a global review on conflicts between livestock and large cats (Khorozyan et al. 2015), our results suggest that the presence of wild prey could reduce livestock depredation by pumas and thus help facilitate coexistence with humans (Hiller et al. 2015; Guerisoli et al. 2017).

As predicted, we also found that pumas preferred areas with a lower density of ranches. Although *P. concolor* is characterized by great ecological plasticity (Nowell and Jackson 1996) and occurs in landscapes dominated by anthropic activities (Riley and Malecki 2001; Scognamillo et al. 2003; Michalski et al. 2006), habitat loss and illegal hunting are the major threats to its populations globally (Logan and Sweanor 2001; Novack et al. 2005; De Angelo et al. 2011) and locally (Guerisoli et al. 2017). In our study area, each property was associated with the continuous or frequent presence of people who may engage in different activities such as livestock breeding, agriculture, logging, and hunting. Thus, the density of properties is an indicator of the intensity of human disturbance (Gálvez et al. 2018). A comparable response to human pressure has been observed in several populations of pumas (e.g., Van Dyke et al. 1986, in Utah and Arizona; Janis and Clark 2002, in Florida; Sweanor et al. 2008, in California) and their prey (e.g., white-nosed coati, *Nasua narica*: Gompper 1995; white-tailed deer, *Odocoileus virginianus*: Kilgo et al. 1998; three

species of peccaries: Altrichter and Boaglio 2004; guanaco, *Lama guanicoe*: Pedrana et al. 2010). The unfavorable effect on prey can reveal itself in several forms, including a reduction in species richness or diversity (Chapin et al. 2000). Thus, it remains unclear to what extent the avoidance by pumas of areas with strong human pressure is a direct effect of disturbance or is a response to the behavior of their prey (Sweanor et al. 2008; Foster et al. 2010).

Vegetation structure, habitat complexity, and the degree of anthropogenic disturbance did not only affect pumas directly in the Espinal, but also through the influence they had on the accessibility and abundance of wild prey (Fig. 3). The negative effect of humans on puma occurrence in our study area is pervasive and extends across a wide range of spatial scales (see also Caruso et al. 2015, 2016).

Activity patterns.—As we expected, and in accordance with several other studies (e.g., Scognamillo et al. 2003; Gutiérrez-González and López-González 2017), pumas in our study area presented a nocturnal and crepuscular pattern of activity. In general, the activity of this species can be affected by the presence of copredators (such as jaguars, *Panthera onca*: Schaller and Crawshaw 1980), the activity of its prey (Scognamillo et al. 2003), and anthropogenic disturbance (Van Dyke et al. 1986; Paviolo et al. 2009). The number of sampling stations where pumas were recorded did not enable us to explicitly test the effect of covariates on this felid's activity patterns. However, considering the absence of copredators and the intense alteration of the natural habitat in central Argentina rangelands, we suggest that puma activity was primarily driven by the avoidance of the part of the day when human activity and the associated mortality risk were the greatest. A similar conclusion was obtained in an adjacent area with comparable habitat (La Pampa province—Zanón-Martínez et al. 2016).

Records of pumas during the daytime were more common in winter than in summer and the frequency of events was very high at night in summer. In the presence of strong anthropogenic disturbance, it is not surprising that the shorter duration of the night in summer forced pumas to concentrate their activity in the dark hours, provoking a high rate of events per hour. However, that does not explain the apparent increase in diurnal activity that we observed in winter. Because most of their prey species (except wild boar, Caruso et al. 2018; plains vizcacha, Llanos and Crespo 1952; and European hare, Canevari and Vaccaro 2007, M. Guerisoli, pers. obs.) are primarily diurnal, it may be advantageous for pumas to hunt not exclusively during the night. We argue that this happened only in winter because of the extremely high daytime ambient temperatures in summer. Felines have limited capability to thermoregulate (West 2005) and high temperatures could force these species to limit activity during those moments of the day and use caves or shady locations, as suggested for pumas in some regions (Astete et al. 2017). It is possible that in summer, due to the elevated temperatures in our study area, pumas and their prey could be avoiding the hottest hours of the day and start their activity at dusk, when temperatures drop.

We conclude that, in the rangelands of central Argentina, puma activity is primarily limited to the night and to the densest and most structured habitats, where more prey species occur and human activity is reduced. Because *P. concolor* is frequently found in rangelands across its wide range, our results contribute to the understanding of the interactions between this felid and humans in areas with similar characteristics. This information is of great utility to develop plans for the conservation and management of puma populations as well as to favor the coexistence of people and wildlife. Our data support the suggestions from a review of puma-livestock conflict in our area (Guerisoli et al. 2017) that it should be possible to reduce predation on livestock by increasing the availability of wild prey and adopting specific husbandry practices, namely, avoiding the use of closed and semiclosed habitats as grazing grounds for sheep and gathering them at night in corrals located in areas near human residences. These conclusions are also in agreement with recent reviews indicating that livestock management is one of the most promising tools to limit livestock depredation, especially by large carnivores (Miller et al. 2016; Eklund et al. 2017; Moreira-Arce et al. 2018).

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SUPPLEMENTARY DATA

Supplementary data are available at *Journal of Mammalogy* online.

Supplementary Data SD1.—Kendall correlation matrix built with the predictive variables to explain the intensity of puma (*Puma concolor*) habitat use in rangelands of central Argentina.

Supplementary Data SD2.—Results of the principal component analysis to construct a new variable that captured habitat structural complexity in the study area ("Hc").

Supplementary Data SD3.—Average (full and conditional average method) of the estimated values of the variables

included in the models explaining the intensity of puma (*Puma concolor*) habitat use with ΔAICc < 2. *Z* value: Wald statistical test. *Pr* (> |z|): *P*.

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