# Daily activity pattern of pumas (*Puma concolor*) and their potential prey in a tropical cloud forest of Colombia

J. C. Cepeda–Duque, B. Gómez–Valencia, S. Alvarez, D. R. Gutiérrez–Sanabria, D. J. Lizcano

**Abstract**

*Daily activity pattern of pumas (*Puma concolor*) and their potential prey in a tropical cloud forest of Colombia.* Ecosystems in the northern Andes face unprecedented habitat loss. Pumas are the top predators in the region and exert key ecological functions, such as population control and resource facilitation. However, little is known about the temporal niche of the species or its effects on behaviour of prey in the tropics. We hypothesized that there is a link between the activity patterns of pumas and their prey in a cloud forest of the Central Andes of Colombia. We installed 61 camera traps to estimate the degree of overlap between the daily activity curves of pumas and seven potential prey species, using conditional kernel density functions. Pumas, armadillos, mountain pacas, and white–eared opossums were mainly nocturnal, with little crepuscular activity and high temporal overlap. Central American agouti, mountain coati, little red brocket deer, and Cauca guan displayed a predominantly diurnal activity and temporal partitioning with pumas. As opportunistic predators, pumas were able to maximize foraging efficiency by preying on the crepuscular and nocturnal species. Conservation of this highland predator will largely depend on the suitable management of its native prey.

Key words: Activity, Behaviour, Colombia, Conservation, Northern Andes, Top predator

**Resumen**

*Patrón de actividad diaria del puma (*Puma concolor*) y sus posibles presas en un bosque nublado tropical de Colombia.* Los ecosistemas de los Andes del Norte afrontan una pérdida de hábitat sin precedentes. Los pumas son el predador superior de la región y ejercen funciones ecológicas claves como el control poblacional y la facilitación de recursos. No obstante, se conoce poco sobre el nicho temporal de la especie y sus efectos en la conducta de sus presas. Nuestra hipótesis es que existe una relación entre los patrones de actividad del puma y de sus presas en un bosque nublado de los Andes centrales de Colombia. Instalamos 61 cámaras trampa para estimar el grado de solapamiento entre las curvas de actividad diaria de los pumas y las de siete presas potenciales utilizando funciones condicionales de densidad de kernel. El puma, el armadillo, la paca de montaña y la zarigüeya de orejas blancas fueron principalmente nocturnos, con escasa actividad crepuscular y un alto solapamiento temporal. El agutí centroamericano, el coatí de montaña, el venado soche rojo y la pava caucana mostraron una actividad predominantemente diurna y una división temporal con el puma. Como predadores oportunistas, los pumas son capaces de optimizar la eficiencia de la alimentación al cazar presas nocturnas y crepusculares. La conservación de este predador superior dependerá en gran medida del manejo sostenible de sus presas autóctonas.

Palabras clave: Actividad, Conducta, Colombia, Conservación, Andes del Norte, Predador tope

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## Introduction

Large felids are considered key drivers of community structure as they have the potential to suppress prey populations and release plants from herbivory pressure (Sergio et al., 2008). To meet their energy requirement, predators have evolved specialized traits to feed on either a diverse guild or a specific type of prey (MacDonald and Loveridge, 2010). Searching for prey can be energetically expensive, especially when they are distributed heterogeneously in the habitat across space and time (MacArthur and Pianka, 1966).

Light changes throughout the 24h cycle drive the activity of a predator to be synchronized with that of its prey so as to increase the probability of encounter (Kronfeld–Schor and Dayan, 2003; Foster et al., 2013; Hernández–Sánchez and Santos–Moreno, 2020). To avoid potential injury by defensive behaviours or morphological armory of the prey, the predator needs to forage while the prey is inactive (Harmsen et al., 2011). Predator activity, however, may decrease due to greater human presence in a given area so as to minimize the risk imposed by encounters with dogs or poachers (Guerisoli et al., 2019). From the prey's perspective, increasing activity during periods when the predator is inactive may decrease the risk of mortality and maximize resource intake (Brown et al., 1999; Kronfeld–Schor and Dayan, 2003). To assess predator–prey interactions from a temporal niche perspective camera traps have proved useful (Harmsen et al., 2011; Foster et al., 2013). Evidence for temporal interactions is expected when camera traps detect convergence–divergence in the distribution of daily activity curves between two or more species (Oliveira–Santos et al., 2013; Frey et al., 2017).

The puma (*Puma concolor,* Linnaeus, 1771) is the most widely distributed felid in the Americas. It can be found from the temperate forests of Canada to the dry Chaco in Argentina (Nielsen et al., 2015). It inhabits a large variety of ecosystems given its wide patterns of movement (mean dispersal distances of 2.2–76.6 km for females and 19.0–139.8 km for males). Its behaviour is elusive (Nielsen et al., 2015) and it is opportunistic in its prey selection (Moss et al., 2016). Nevertheless, habitat loss, retaliatory killing, and illegal hunting have led to continual declines in its populations and local extinctions (Nielsen et al., 2015).

In the Andes, pumas have been intensively studied at the southern extreme of their range (Walker and Novaro, 2010). Most studies have focused on trophic ecology (Rau and Jiménez, 2002; Osorio et al., 2020), resource selection (Elbroch and Wittmer, 2013; Gelin et al., 2017), habitat use (Quiroga et al., 2016), human–wildlife conflicts (Kissling et al., 2009; Ohrens et al., 2016), population density (Guarda et al., 2017) and temporal activity pattern (Lucherini et al., 2009; Osorio et al., 2020). In the Northern Andes, the natural history, ecology and behaviour of pumas remain largely unknown. In the Central Andes of Colombia, pumas are the dominant predator in the cloud forests and paramos (Castillo et al., 2020) and the few available studies describe puma feeding habits (Hernández–Guzmán et al., 2011; Jaimes et al.,

2018; Castillo et al., 2020), habitat use (Boron et al., 2019), human wildlife conflicts (Valderrama–Vásquez et al., 2016), spatiotemporal coexistence with jaguars (Figel et al., 2021), and activity patterns (Zapata–Ríos and Branch, 2016; Ramírez–Mejía and Sánchez, 2016; Cáceres–Martínez et al., 2016). Currently, studies about pumas and prey activity patterns in this ecoregion are lacking, preventing elucidation of the temporal strategies underpinning the survival of this predator (Soria–Díaz et al., 2016).

Our goal was to describe the activity patterns of pumas in a cloud forest of the Central Andes of Colombia and assess their relationship with the activity patterns of seven prey species: Central American agoutis, white–eared opossums, mountain coatis, mountain pacas, armadillos, little red brocket deer, and Cauca guans. We hypothesized that to maximize encounters, pumas will present a greater temporal overlap of activity with their presumed favoured prey in the region.

## Material and methods

The study was conducted on the western slope of the Central Andes of Colombia, within a forest remnant in the 3,986 ha Ucumari Natural Regional Park and the southern portion of the 21,131 ha Campoalegre Soil Conservation District (fig. 1). Forests within these protected areas were strongly degraded during the early twentieth century. Before the protected area was established, cattle ranching was widespread, even on steep slopes (up to 45º), relegating the forest to yet steeper terrain (Murcia, 1997). In the 1960s, local farms were acquired by the regional public authorities and reforestation efforts were conducted at various sites for soil and watershed protection (Kattan et al., 2006). As part of this program, plantations of Chinese ash (*Fraxinus chinensis*) were established in degraded lands along the upper portion of the middle Otún basin (Kattan et al., 2006). A large strip was planted in the valleys and later abandoned for secondary recovery (Rangel, 1994). Currently, a mixture of native secondary forest patches remains, forming a complex habitat mosaic of native cloud forest trees, Chinese ash, Colombian pine (*Podocarpus oleifolius*), Andean alder (*Alnus acuminata*), and exotic pine (*Pinus patula*) plantations (Lentijo and Kattan, 2005; Murcia, 1997). The region has a bimodal precipitation pattern with the rainiest seasons occurring between March–May and October–November, respectively. Elevation in the zone ranges from 1,750 to 2,600 m (Kattan et al., 2006). The average annual temperature is 14 ºC (range 12–18 ºC) and the average annual relative humidity is 87 % (Corporación Autónoma Regional de Risaralda, 2000).

We placed 61 camera traps (Bushnell Trophy Cam HD), originally to monitor mountain tapir (*Tapirus pinchaque,* Roulin, 1829) populations at a maximum distance between stations of 500 m following the TEAM protocol (TEAM Network, 2011). Cameras were placed at a height of 40 cm above ground level along natural trails and distanced at least 50 m from the main trails

to minimize theft (Kelly et al., 2012). The cameras were set to record a sequence of three pictures with a trigger interval of 1 second; no lures were used. The sampling period encompassed four months during the dry season, from December 2016 to March 2017, with a total sampling effort of 3,070 traps/nights.

In the Central Andes, the northern pudu (*Pudu mephistophiles,* Winton, 1986) is the most consumed prey by pumas, accounting for 57 % of its diet. This is followed by the forest rabbit (*Silvilagus brasiliensis*, Linnaeus 1758), 54 %; mountain coati (*Nasuella olivacea*, Gray, 1865), 27 %; white–eared opossum (*Didelphis pernigra*, Allen, 1900), 10 %; little red brocket deer (*Mazama rufina*, Pucheran, 1851), 9 %; and mountain paca (*Cuniculus taczanowskii*, Stolzmann, 1865), 8 % (Hernández–Guzmán et al., 2011; Castillo et al., 2020). In the Eastern Andes, the most frequently consumed prey within the puma's diet are  the brown–nosed coati (*Nasua nasua,* Linnaeus 1776), representing 20 % of the diet, followed by the little red brocket deer, 13 %; mountain paca, 11 %; armadillo (*Dasypus novemcinctus,* Linnaeus, 1758), 5 %; common opossum (*Didelphis marsupalis*, Linnaeus, 1758), 5 %; and Central American agouti (*Dasyprocta punctata,* Gray, 1842), 3 % (Jaimes et al., 2018).

In the current analysis, we did not include data of northern pudu, brown–nosed coati, or forest rabbits due to the small sample size (n = 0–10 captures). We included the Cauca guan (*Penelope perspeicax,* Bangs, 1911) as potential prey for pumas based on a previous anecdotal report on the likely consumption of this endangered and endemic cracid near the protected area (Ríos et al., 2006). Cauca guans could be a potential prey item for pumas as these birds have ground–dwelling habits, and conspicuous behaviors. Furthermore, populations in the protected area reach the highest densities within its known geographical range (10–40 ind/km$^2$), especially during the dry season (Kattan et al., 2014).

To describe the activity patterns of pumas and their potential prey, we considered all consecutive records of a species obtained in 60 minutes as a single, independent event (Di Bitetti et al., 2006; Ridout and Linkie, 2009; Oliveira–Santos et al., 2013; Zanón Martínez et al., 2016). We assigned each independent event to one of the following periods: day (from 1 h after sunrise to 1 h before sunset), night (from 1 h after sunset to 1h before sunrise), dusk (from 1 h before sunset to 1 h after sunset), and dawn (from 1 h before sunrise to 1 h after sunrise) (Monterroso et al., 2014). We classified species as diurnal or nocturnal depending on whether their activity was concentrated within daylight or night–time hours, respectively. Habits were considered crepuscular if the species were mostly detected during the dawn and dusk hours. If a species showed no tendencies of activity for a given period, it was classified as cathemeral (van Schaik and Griffits, 1996).

For each species, we transformed hours and minutes of single detection events into circular data and obtained the mean, standard deviation, and the 95 % confidence intervals of the activity patterns using a von Mises distribution (Avendaño, 2019). To assess whether the activity patterns were randomly dispersed throughout the 24 cycles, we used the Rao Spacing test, which is more sensitive to non–unimodal distributions (Avendaño, 2019).

We used a non–parametric model of kernel density function to estimate activity curves and the degree of overlap between pumas and their prey (Oliveira–Santos et al., 2013; Monterroso et al., 2014). The density of activity records for a species is measured as a continuous distribution of probabilities throughout the 24h cycle (Frey et al., 2017). These models assume that while a species is active, it has the same probability of being detected in the camera traps at any time in the day (Linkie and Ridout, 2011). We conducted pairwise comparisons of puma activity patterns and those of their prey by using the conditional overlap coefficient $\Delta_1$ for small samples (Ridout and Linkie, 2009). This coefficient has a range of 0 (no overlap) to 1 (complete overlap) and is obtained by taking the minimum value of the density functions of two daily cycles that are compared at each time point and represented as the overlapped area occupied by two specific density curves (Ridout and Linkie, 2009). To calculate the accuracy of the $\Delta_1$ estimator, we used the confidence intervals of the 1,000th bootstrap sample (Ridout and Linkie, 2009). The choice of a given conditional density isopleth can affect the interpretability of the overlap measures derived from two kernel estimators (Frey et al., 2017). For instance, the 95% density isopleth accounts for the whole temporal range where animal activity takes place, whereas the 50% isopleths account for its peak activity (Oliveira–Santos et al., 2013). Under a conditional density function, we estimated both the 95 % and 50 % isopleths to determine the 'activity range' and 'activity core', respectively, from the time records (Oliveira–Santos et al., 2013). Finally, we searched for dispersion of activity throughout the daily cycle between pumas and prey using the Watson Two–test, with a significance level of 5 %. The analysis was carried out using the circular and overlap packages (Meredith and Ridout, 2014) in the R software (R Core Team, 2017).

## Results

Our sampling effort in the Ucumari Regional Natural Park and the southern portion of the Campoalegre Soil Conservation District yielded a total of 1,445 independent records corresponding to 66 vertebrate species, 33 mammals and 33 birds. Overall, pumas accounted for only 9% of the detections during our four survey months. Some prey,  such as the Cauca guan (21 %), the mountain coati (18 %), little red brocket deer (18 %), white–eared opossum (12 %) and armadillo (12 %) were better represented, whereas other species, such as the Central American agouti (5 %) and the mountain paca (3 %) accounted for a lower number of detections (table 1).

We obtained 39 independent puma records and the most frequently detected potential prey were the Cauca guan, mountain coati, and little red brocket deer with 84, 71, and 64 records respectively, followed by armadillos with 51 records,
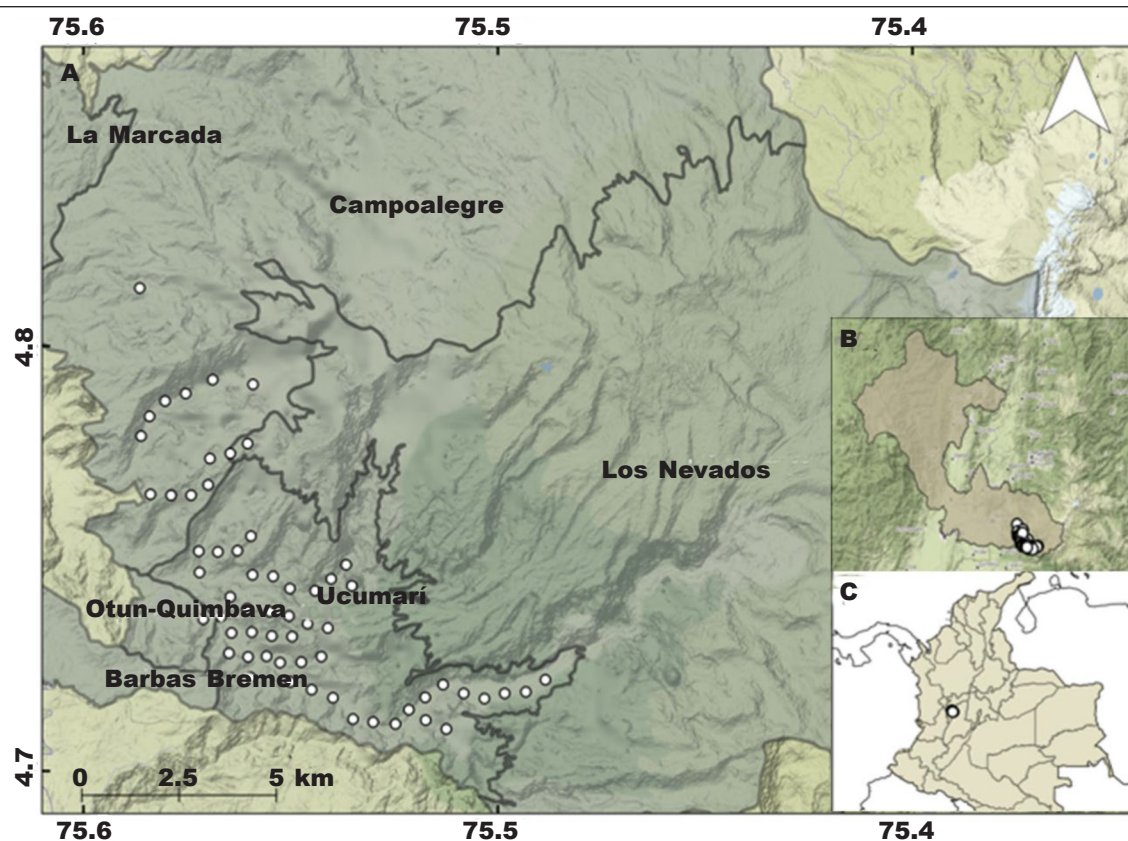
Fig. 1. Map of the camera trap survey conducted from 16 December 2016 to 20 March 2017 located at Ucumari Regional Natural Park and Campoalegre Soil Conservation District (A), Risaralda department (B), Colombia (C): white dots represent the camera trap stations.

*Fig. 1. Mapa del estudio realizado con cámaras de trampeo entre el 16 de diciembre de 2016 y el 20 de marzo de 2017 en el Parque Natural Regional Ucumari y el Distrito de Conservación de Suelos Campoalegre (A), en el departamento de Risaralda (B), Colombia (C): los puntos blancos representan las estaciones de fototrampeo.*

white–eared opossums with 50 records, Central American agoutis with 22 records, and mountain pacas with 12 records.

Puma activity was predominantly nocturnal or crepuscular. The onset of activity was late afternoon (17:00–18:00 h), peaking early in the night (20:00–22:00 h) and decreasing before sunrise (01:00–05:00 h). Subtle increases in puma activity were recorded during the day, especially at midday and early afternoon (12:00–13:00 h). Regarding the activity patterns of prey, the Cauca guan, mountain coati, and Central American agouti were primarily diurnal, and the white–eared opossum, mountain paca, and armadillo were mainly nocturnal (fig. 2). Cauca guans were the only species with activity mainly around noon (11:0–12:00 h), with a decreasing trend towards sunrise and sunset (fig. 2A). The activity of Central American agoutis started in the early morning (07:00–09:00 h), decreased around midday (11:00–12:00 h) and peaked near dusk (16:00–18:00 h).

Little red brocket deer were mostly diurnal and crepuscular (fig. 2F), with two activity peaks, one during the morning with periodic increases in the early (07:00–09:00 h) and late morning (10:00–11:00 h). The other peak was around the afternoon and dusk (14:00–18:00 h). Mountain coatis also showed two distinct peaks, one in the late morning (10:00–11:00 h) and the other between the early afternoon and dusk (14:00–18:00 h). White–eared opossums showed a predominant crepuscular activity, with a distinctive peak at dusk (18:00–19:00 h) that dramatically decreased during early night hours (20:00–23:00 h) before increasing again at midnight (fig. 2E). Armadillos and mountain pacas showed two distinctive nocturnal peaks, one concentrated before midnight (21:00–23:00 h) and one after midnight (00:00–02:00 h), with a gap in its activity between the two periods (fig. 2). Circular central tendency measures and directionality tests for the activity records of each species are provided in table 1.

Table 1. Activity patterns of pumas and their prey in a cloud forest of the Central Andes, Colombia. Number of 60–minute independent events (IE), mean and circular deviation (SD) from the activity vectors of each species are shown. Confidence intervals (CI) and the Rao (U) test were set at an alpha = 0.05.

*Tabla 1. Patrones de actividad del puma y de sus presas en un bosque nuboso de los Andes centrales, Colombia. Se indican el número de episodios independientes de 60 minutos (IE), la media y la desviación estándar circular (SD) de los vectores de actividad de cada especie. Los intervalos de confianza (CI) y la prueba de Rao (U) se calibraron a un alfa = 0,05.*

| Species | IE | Mean (SD) | CI (95%) | U–test | *P*–value |
|---|---|---|---|---|---|
| Puma | 39 | 20:35 (01:49) | 01:39–14:22 | 131.47 | > 0.001 |
| Cauca guan | 84 | 11:30 (00:37) | 10:55–12:01 | 222.77 | < 0.001 |
| Central American agouti | 22 | 13:19 (00:57) | 11:28–15:03 | 200.64 | < 0.001 |
| Mountain coati | 71 | 12:54 (00:59) | 11:48–13:54 | 187.28 | < 0.001 |
| Armadillo | 51 | 23:31 (00:56) | 22:20–00:33 | 202.95 | < 0.001 |
| White–eared oppossum | 50 | 22:32(00:56) | 21:25–23:43 | 221.25 | < 0.001 |
| Mountain paca | 12 | 23:09 (00:42) | 21:19–00:40 | 216.15 | < 0.001 |
| Little red brocket deer | 64 | 12:54 (00:52) | 11:59–13:47 | 180.82 | < 0.001 |

Coefficients of overlap in the temporal activity patterns varied according to the range and core activity (table 2). We noted a higher overlap of activity between pumas and nocturnal prey species than between pumas and diurnal species (fig. 2). Cauca guans, Central American agoutis, and mountain coatis with a mostly diurnal temporal activity, exhibited low overlap with puma activity patterns (table 2). Regarding to temporal partitioning, we found statistical differences in all the paired associations between the activity patterns of pumas vs. Cauca guans ($U^2$ = 1.2125, P < 0.001), vs. Central American agoutis ($U^2$ = 0.4061, P < 0.001), vs. mountain coatis ($U^2$ = 0.6772, P < 0.001), vs. little red brocket deers ($U^2$ = 0.7031, P < 0.001), vs. mountain pacas ($U^2$ = 0.2207, P < 0.001), vs. armadillos ($U^2$ = 0.3415, P < 0.001), and vs. white–eared opossums ($U^2$ = 0.3125, P < 0.001).

## Discussion

We assessed the daily activity of pumas and their prey within a well–preserved Andean Forest in which other large predators such as jaguars (*Panthera onca,* Linnaeus 1758) are absent. Pumas showed a nocturnal and crepuscular activity that is geographically consistent with studies made in other Neotropical areas (Scognamillo et al., 2003; Monroy–Vilchis et al., 2009; Harmsen et al., 2009; Blake et al., 2012; Foster et al., 2013; Zanón Martínez et al., 2016; Cáceres–Martínez et al., 2016; Porfirio et al., 2017; Azevedo et al., 2018; Guerisoli et al., 2019; Osorio et al., 2020). Therefore, factors other than habitat features (such as human disturbance and prey availability) may more likely drivers of the puma's activity patterns (Harmsen et al., 2011; Suraci et al., 2019). In view of the small sample size, the puma activity

patterns we observed should be interpreted with caution. Furthermore, we were unable to discriminate between sexes in our records. Recent research emphasized it is necessary to have more than 100 records to reduce bias in $\Delta_1$ estimates (Lashley et al., 2018) and that there are intersexual differences in puma activity, with males being more nocturnal and crepuscular and females more cathemeral (Azevedo et al., 2018).

Regarding diurnal prey, our results for mountain coatis differed from reported populations in the Central and Eastern Andes (Ramírez–Mejia and Sánchez, 2016, Cáceres–Martínez et al., 2016) of Colombia, and the Tabaconas Namballe reserve in Peru (Mena and Yagui, 2019) where they are primarily nocturnal. This could be attributed to a behavioral strategy to avoid potential intraguild predation by pumas (Castillo et al., 2020), and feral dogs (Mena and Yagui, 2019). Evidence from the Central Andes of Ecuador (Zapata–Ríos and Branch, 2016) suggests that the presence of feral dogs around the protected areas can deplete mountain coati abundance. Yet given the low number of dogs (n < 5 observed during our survey, we opted to exclude them from our inferences to avoid skewed comparisons (Mena and Yagui, 2019). When compared with other procyonids, coatis have an extra cone–class on their retinas, which confers them dichromatic colour vision (Jacobs and Deegan, 1992). Greater activity during diurnal hours may thus increase their visual perception and feeding intake while foraging on the forest floor (Whiteside, 2009). Moreover, diurnal activity in coatis prevents heat loss while foraging, and foster social interactions by increasing intraspecific recognition (Costa et al., 2009; Mena and Yagui, 2019).

Central American agoutis showed a diurnal behaviour, concentrated in the early morning and the late afternoon. This observation matches findings from
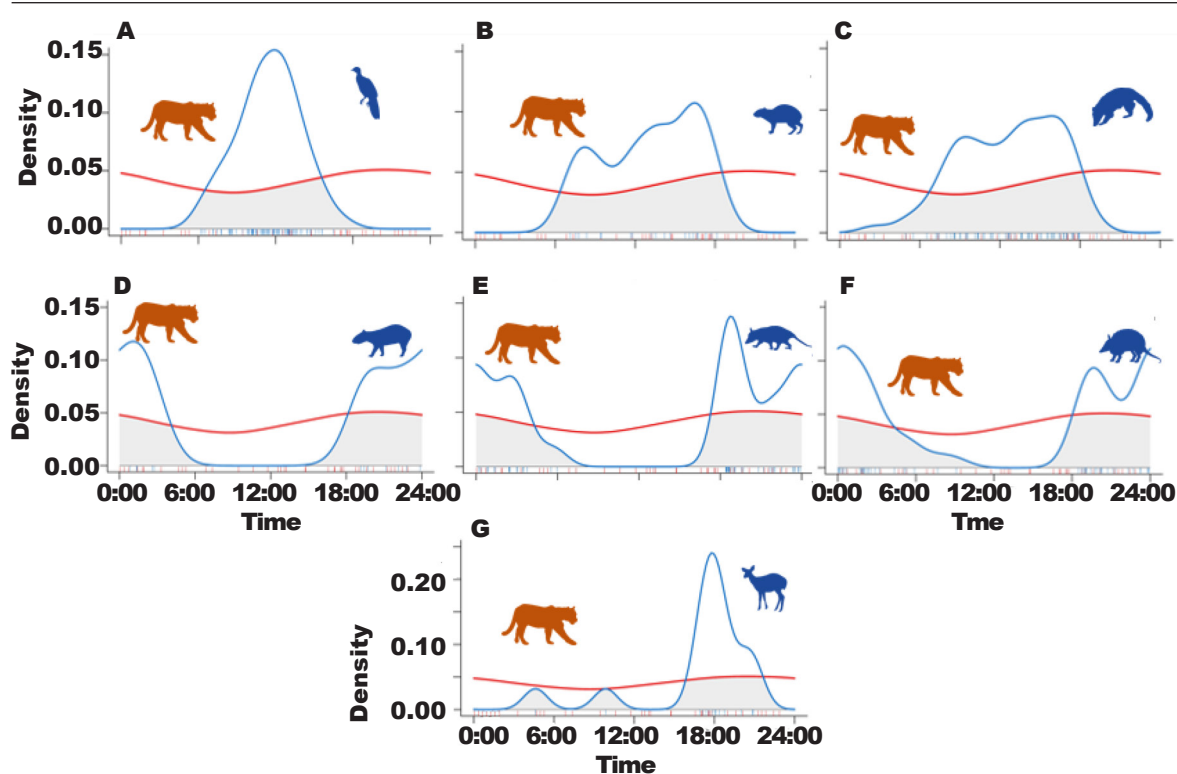
Fig. 2. Activity patterns and degree of overlap between pumas (red line) and prey (blue line) at the Ucumari Regional Natural Park and the Campoalegre Soil Conservation District: A, Cauca guans; B, Central American agoutis; C, mountain coatis; D, mountain pacas; E, white–eared opossums; F, armadillos; G, little red brocket deer. *(The shaded area represents overlap*; from December 2016 to March 2017 we obtained 393 independent activity records for pumas and prey from 3,070 trap/nights.)

*Fig. 2. Patrones de actividad y grado de solapamiento entre el puma (línea roja) y sus presas (línea azul) en el Parque Natural Regional Ucumari y el Distrito de Conservación de Suelos Campoalegre: A, pava caucana; B, agutí centroamericano; C, coatí de montaña; D, paca de montaña; E, zarigüeya de orejas blancas; F, armadillo; G, venado soche rojo. (El área sombreada reprresenta el solapamiento; entre diciembre de 2016 y marzo de 2017 obtuvimos 393 registros independientes de actividad para pumas y sus presas con un esfuerzo de 3.070 trampas noche.)*

previous studies in the tropical rainforests of Mexico (Mendoza et al., 2019), Panamá (Suselbeek et al., 2014), the Brazilian Amazon (Gómez et al., 2005), and the Central Andes of Colombia (García–R. et al., 2019). This diurnal behaviour in Central American agoutis could increase its success in searching for seeds while avoiding the midday heat (Suselbeek et al., 2014; Duquette et al., 2017). Cauca guans were the only species whose activity peaked at midday and decreased towards the sunset and sunrise hours. Populations of this endemic cracid migrate from adjacent forests in the region during the dry season (November–December) to forage on Chinese Ash leaves (Muñóz et al., 2007), which provide more food than native trees (Kattan et al., 2014). In these open plantations, up to 30 individuals of Cauca guans have been observed foraging at a single location and the open canopy can increase their exposure to predators

(Muñóz et al., 2007). Thus, being active at the hottest hours of the day when pumas are less active might reduce predation risk. Likewise, terrestrial habits in this guan are linked to opportunistic foraging on army ants (*Labidus praedator),* and increased activity during midday hours could increase resource intake when other birds are less active (Rios et al., 2008). The diel activity of little red brocket deer that we observed to peak in the morning is consistent with the activity patterns found for this species in cloud forests and paramos of Ecuador (Zapata–Ríos and Branch, 2016). However, it differs from the findings for a neighbouring region, which showed a greater increase in activity during crepuscular hours (Ramírez–Mejía and Sánchez, 2016). Our results depart from the phylogenetic signal in activity observed towards nocturnality for other red *Mazama* species (Oliveira et al., 2016) such as the South American red brocket deer (*M. americana,*

Table 2. Overlap estimates at the range (0.95) and core (0.50) activity for the paired associations of pumas and prey in the Ucumari Regional Natural Park and the Campoalegre Soil Conservation District, Central Andes, Colombia. We obtained an additional overlap estimate by resampling the transformed data at 1,000 iterations. Confidence intervals of the overlap coefficients were set at an alpha = 0.05.

*Tabla 2. Estimación del solapamiento en el período total de actividad (0,95) y el período de actividad máxima (0,50) para las asociaciones pareadas de pumas y sus presas en el Parque Natural Regional de Ucumari y el Distrito de Conservación de Suelos Campoalegre, en los Andes centrales, Colombia. Obtuvimos una estimación adicional de solapamiento al volver a muestrear los datos transformados con 1.000 iteraciones. Los intervalos de confianza de los coeficientes de solapamiento se calibraron a un alfa = 0,05.*

| Species pair | $\Delta_1$ (0.95) | $\Delta_1$ (0.50) | $\Delta_1$ resampled | CI (95%) |
|---|---|---|---|---|
| Puma vs. Cauca guan | 0.35 | 0.01 | 0.42 | 0.23–0.51 |
| Puma vs. Central American agouti | 0.51 | 0.15 | 0.54 | 0.34–0.66 |
| Puma vs. mountain coati | 0.51 | 0.07 | 0.56 | 0.37–0.67 |
| Puma vs. armadillo | 0.68 | 0.50 | 0.63 | 0.49–0.78 |
| Puma vs. white–eared opossum | 0.69 | 0.63 | 0.60 | 0.46–0.73 |
| Puma vs. mountain paca | 0.58 | 0.44 | 0.54 | 0.35–0.72 |
| Puma vs. little red brocket deer | 0.47 | 0.01 | 0.47 | 0.25–0.68 |

Erxleben, 1777), the Brazilian dwarf brocket deer (*M. nana*, Hensel, 1872), and the small red brocket deer (*M. bororo,* Duarte, 1996). Deer are central taxa within the puma's diet (Ackerman, 1982), and the diurnal behaviour observed for little red brocket deer may reflect behavioural avoidance of encounters with this and other predators (Zapata–Ríos and Branch, 2016). Additional constraints in the activity of little red brocket deer may be attributed to resource partitioning with other sympatric ungulates (Blake et al., 2012) and thermal constraints related to closed habitats (Oliveira et al., 2016).

Nocturnal prey species like white–eared opossums showed an activity pattern that is congruent with other studied populations of the Central (Ramírez–Mejía and Sánchez, 2016) and Eastern Andes (Cáceres–Martínez et al., 2016) of Colombia, and the Central Andes of Ecuador (Zapata–Ríos and Branch, 2016). As white–eared opossums can exploit various human–related resources, its nocturnal and arboreal activity allows it to minimize encounters with humans and dogs (Zapata–Ríos and Branch, 2016). Mountain pacas showed a nocturnal activity consistent with previous studies in Perú (Jiménez et al., 2010) and the Central Andes of Colombia (Ramírez–Mejia and Sánchez, 2016). This large rodent has historically been hunted by humans for its meat, even within protected areas where poaching is practically absent; its nocturnal behaviour could be a conditioned response to the presence of humans and dogs (Zapata–Ríos and Branch, 2016).

Our initial hypothesis of temporal overlap between puma and prey was supported only by armadillos and white–eared opossums, two nocturnal mammals frequently targeted by this predator in the region (Castillo et al., 2020). This pattern is consistent with other studies where pumas adjust their activity to decrease the energy costs of searching for food (Scognamillo et al., 2003; Harmsen et al., 2011; Foster et al., 2013; Zanón Martínez et al., 2016; Azevedo et al., 2018; Osorio et al., 2020).

Moreover, it has been reported that higher nocturnality of predators in areas with intense human activity can create temporal human shields for locally abundant prey by reducing its perceived risk of predation (Gaynor et al., 2018; Suraci et al., 2019). In the Pampas (Zanón Martínez et al., 2016) and Triangulo Mineiro regions (Azevedo et al., 2018) pumas were found to be strictly nocturnal in areas with higher diurnal activity of humans. A trail that longitudinally crosses the Ucumarí Natural Regional Park is frequently visited by tourists and local farmers, mostly during daytime (Rangel, 1994). Within the park, mountain coatis, little red brocket deer, and Cauca guans have the potential to reach high densities (Kattan et al., 2014; unpublished data), which may increase their predation risk (Osorio et al., 2020). Thus, despite being common in our survey, the temporal partitioning of mountain coatis, little red brocket deer, and Cauca guans can decrease the predation pressure exerted by pumas. The theory of limiting similarity (Abrams, 1983) states that coexistence within assemblages or communities drives differences among one or more niche dimensions (but see Jaksić, 1982). Further understanding of how the shared use of the light hours can drive competition is needed to determine future conservation actions.

Some relevant prey in the diet of puma populations from the Northern Andes, such as the northern pudu, and forest rabbit, were rare in our survey (Hernández–Guzman et al., 2011; Castillo et al., 2020). More research focused on the puma feeding habits in these

Andean forests is needed to reliably couple temporal predator–prey relationships with trophic interactions (Azevedo et al., 2018).

Historically, the Andean region has been characterized by a prevalence of human activities that have caused dramatic changes in the natural heritage of Colombia (Sánchez–Cuervo et al., 2012). As mentioned above, human–mediated fear in pumas may reduce the range of prey they can reach when compared to the entire diversity of prey taxa available (Suraci et al., 2019; Blecha et al., 2018; Wilmers et al., 2013). More rigorous assessment on the spatial and temporal niche of both the puma and its available prey assemblage, perhaps using radio telemetry, should be carried out to confirm our results.

The conservation of forested habitats is critical for the puma's survival and the maintenance of its prey base (Paviolo et al., 2018). Puma activity patterns were mainly nocturnal in our study, and given its opportunistic foraging behaviour, we suggest that the more nocturnal potential prey will be more relevant as a feeding resource. Although armadillos and white–eared opossums provide less biomass (3–7 kg and 1–6 kg, respectively) for pumas when compared with larger prey such as the little red borcked deer (11 kg) (Hernández–Guzmán et al., 2011; Foster et al., 2013) we suggest that, even within the protected area, human activities (trekking, unmanaged tourism) may create a landscape of fear that constricts the trophic niche of the puma to less nutritive prey (Suracy et al., 2019). We found that activity overlap analysis was a very useful (albeit complementary) approach to suggest likely key prey items for pumas when dietary studies are lacking (Azevedo et al., 2018).

Several important questions remain unsolved. For instance, how can tourism within these protected areas influence the puma's prey selection, hunting success, and energy intake? And are there any seasonal or intersexual differences in the temporal overlap between pumas and prey in these threatened highland forests? Finding answers to these questions will be key for the development of management and conservation measures and for the protection of the remaining puma populations and wildlife that share the tropical cloud forests.

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