



Original Investigation

Jaguar and puma activity patterns in relation to their main prey

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ABSTRACT

Activity patterns of top predators are adapted for efficient predation, whereas their prey must contend with the conflicting demands of acquiring resources and avoiding predators. Here we analyse the activity of jaguars (*Panthera onca*) and pumas (*Puma concolor*) in relation to their most important prey species, armadillos (*Dasypus novemcinctus*) and pacas (*Agouti paca*) respectively, in the Cockscomb Basin Wildlife Sanctuary, Belize using large-scale camera-trap data. Jaguars and pumas have similar 24 h activity patterns as armadillos and pacas, both burrow-dwelling species, and negligible overlap with less frequently consumed prey species such as red brocket deer (*Mazama americana*) and peccaries. Activity of armadillos and pacas varied with moon phase, with reduced activity during periods of brighter illumination, perhaps as a predator-avoidance strategy. Across the study area, moon phase had no overall influence on jaguar and puma activity; however at locations associated with armadillos, jaguar activity declined with brighter illumination, perhaps indicating a shift to alternative prey during full moon when armadillos avoided foraging above ground. No such relationship was found for pumas and moon phase at locations associated with pacas.

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Introduction

Predator-prey dynamics are regulated by predator hunting ability, and the predator-avoidance strategies of their prey. Predators can maximise the pay-off for hunting by doing so when prey are most vulnerable to attack. For example, non-burrowing carnivores hunt burrowing species when they feed above ground, whereas burrowing carnivores specialise in hunting burrowing species when they are below ground (Fedriana et al., 1999). The activity patterns of the predators coincide with periods when the prey are most vulnerable. Conversely, prey species may change their daily activity patterns to avoid predation (e.g. Eccard et al., 2008; Gliwicz and Dabrowski, 2008). Opportunistic wide-ranging predators, whose geographic ranges encompass multiple prey species, locally adapt their activity patterns to those of the prey. For example, the leopard (*Panthera pardus*) is nocturnal across most of its African savannah range but is mainly diurnal in West African rainforest areas in accordance with the activity patterns of prey (Jenny and Zuberbuhler, 2005).

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Cats hunt primarily by auditory and visual cues (Kitchener, 1991; Sunquist and Sunquist, 2002) therefore they are more likely to detect and hunt actively foraging animals than inactive animals. Night-time illumination varies through the cycle of moon phases, with a fuller moon increasing visibility for cats and the vulnerability of their prey. Some rodent species are known to alter their activity patterns in relation to moon phase, trading foraging efficiency for lowered susceptibility to predation on bright nights (Lockard and Owings, 1974; Emmons et al., 1989; Wolfe and Summerlin, 1989; Daly et al., 1992; Kotler et al., 2004). Our study compares the activity patterns of jaguars (*Panthera onca*) and pumas (*Puma concolor*), two similar-sized sympatric cats, with their mammalian prey, in Belize, Central America by analysing data derived from one of the largest camera-trap studies conducted in the Neotropics.

Jaguars and pumas have low dietary overlap in Belize. Foster et al. (2010) found that they both mainly eat medium-sized (5–10 kg) burrow-dwelling mammals: jaguars favouring armadillos (*Dasypus novemcinctus*, 50% relative occurrence, 50% biomass), and pumas favouring pacas (*Agouti paca*, 60% relative occurrence, 50% biomass). Although jaguars also ate pacas and pumas ate armadillos, they were taken at low levels (5% and 7% respectively). In other areas of Mesoamerica wild ungulates are often major prey species of jaguars and pumas (Aranda and Sanchez-Cordero, 1996; Núñez et al., 2000; Scognamiglio et al., 2003). Large ungulate species occur in Belize (tapir; *Tapirus bairdii*, white-lipped peccary; *Tayassu*

pecari, collared peccary; *Tayassu tajacu* and red brocket deer; *Mazama americana*), but they are less important in the cats' diets contributing, in combination, to less than one-quarter of the diet of either cat species.

The reliance of both cats on these smaller species does not seem to be detrimental since the density of jaguars is one of the highest in the world at close to 10 individuals per 100 km² (Silver et al., 2004; Harmsen, 2006). Although living at an unknown lower density than jaguars, CBWS has a healthy sympatric puma population (Harmsen et al., 2010). A relatively high number of puma photographs were recorded per survey period. A substantial percentage of these photographs could not be identified to individual level, making it impossible to estimate puma densities using mark-recapture analysis like Kelly et al. (2008) (Harmsen et al., 2010).

Jaguars and pumas both have nocturnal activity patterns in Belize (Harmsen et al., 2009). We tested whether the activity patterns of these cat species are synchronised to the activity pattern of their principal prey. As there are no burrowing mammalian predators in the region (Reid, 1997), pacas and armadillos may face a trade-off between above-ground foraging and refuge from cat predation. Armadillos and pacas may reduce their above-ground activity on bright nights when the risk of detection by jaguars and pumas may be greatest. We tested whether activity is influenced by night-time illumination (moon phase) compared to the activity of non-burrowing nocturnal species which endure no predation pressure from jaguars and pumas. If prey activity cycles with moon phase, so too may predator activity. If prey remain for longer below ground on bright nights, jaguars and pumas may become more active to compensate for lowered availability of their primary prey, or they may lower their activity to save energy for more efficient hunting during darker nights, or they may switch to diurnal prey during this period.

Material and methods

The study was conducted in the eastern lowlands of the Cockscomb Basin Wildlife Sanctuary (CBWS) in Belize, Central America (UTM WGS84 03.48.113, 18.54.515). The CBWS covers 425 km² of protected secondary tropical moist broad-leaf forest. CBWS supports a high density of jaguars, ~8–10 jaguars per 100 km² (Silver et al., 2004; Harmsen, 2006; Foster, 2008). The density of pumas is unknown, but small-scale, short-term recognition from camera data was possible and suggested that pumas exist at lower numbers than jaguars in this area (Harmsen et al., 2010). The CBWS has a high density of waterways (~2.5 km/km²). Within the homogeneous secondary growth of the eastern basin, photo capture rates of jaguars and pumas do not vary with distance to water, altitude or slope (Harmsen et al., 2010).

A total of 110 camera locations functioned for periods of 2–20 months over 2.5 years. The camera study took place in the same area and period of the diet study of Foster et al. (2010). Cameras were located along old logging roads, newly cut trails and waterways (Fig. 1). The cameras covered an effective sampling area of 198 km² (Harmsen, 2006). Neighbouring cameras were separated by 0.5–2.0 km, with a maximum distance between any two cameras of 21.6 km (mean ± SD = 7.9 km ± 4.3, $n = 110$, Fig. 1). At each location, a pair of passive cameras (Cam Trak South Ltd) was set to photograph each flank of any passing animal, with continuous 24-h operation and an enforced 3-min delay between consecutive photographs. All photographs were stamped with the time and date. This study derives its camera-trap data from multiple surveys carried out from 2003 to 2005 (Silver et al., 2004; Harmsen, 2006; Harmsen et al., 2009, 2010). Analyses were based on 32 jaguars and at least 9 pumas.

Activity patterns were extracted from the camera data for jaguars, pumas, the two major prey species (armadillos and pacas), three ungulate prey species (red brocket deer, collared peccaries and white-lipped peccaries) and three control species. The control species were included to test whether activity varied with moon phased in non-prey species: a medium-sized carnivore, the ocelot (*Leopardus pardalis*), a medium-sized omnivore, the common opossum (*Didelphis marsupialis*), and a large herbivore, the tapir. Statistics were calculated with Minitab version 14.

Activity patterns

The 24-h activity patterns all species were deduced from camera-trap photo records (see Harmsen et al., 2009). Pearson correlations were calculated between the 24-h activity patterns of jaguars and pumas and the activity patterns of each prey species to assess the level of association in activity. Percentages were Arcsine-root transformed prior to analysis.

Moon phase and activity

Moon phase was enumerated for each calendar day of the sampling period using the software Quickphase Pro 3.3.4 (BlueMarmot.com). On average, a complete moon phase cycle lasts 15 days (13–16 days). To standardise for variation in length, moon phase was scaled on a 15-point scale from 0 = new moon to 14 = full moon, with first and last quarter moon both = 7. Percent capture success of each species was calculated for each moon-phase level as (species capture frequency/trap effort × 100). Linear regressions were calculated for capture success of each nocturnal species against moon phase after arcsine transformation.

Cloud cover varied within and between nights, and its effects on lunar illumination could not be measured at camera locations. The analyses therefore assumed that cloud cover would only weaken existing relationships between moon phase and activity.

Previous camera-trap studies in CBWS (Weckel et al., 2006; Harmsen et al., 2010) showed that armadillos and pacas are captured in different locations than jaguars and pumas. While the cats were mainly caught on open trails, the two prey species were mostly captured in dense undergrowth. Such variation in optimal capture locations of different species does not compromise studies of activity patterns as long as the sample size for each species is high enough; and may usefully indicate locations where the predators are most likely to encounter their prey and be actively hunting, versus simply travelling. It was assumed that jaguars and pumas were hunting in locations associated with high armadillo and paca activity, and they were more likely to be travelling when active on wide trails where armadillos and pacas are less common. We therefore repeated the analysis between moon phase and activity for a subset of locations associated with paca and armadillo captures (≥ 2 captures/100 days).

Results

Activity patterns

Red brocket deer and both peccary species had diurnal activity patterns, the converse of the activity pattern of the two large cats (Fig. 2). The activity patterns of armadillos, pacas and tapirs overlapped with the nocturnal habits of the two large cats. Paca and tapir activity correlated positively with the activity patterns of jaguars and pumas (Table 1). Although armadillo activity did not correlate with the activity of either cat, the activity of the jaguars, pumas and armadillos overlapped for 10 h of the night. Activity patterns of both cats were correlated with the three species not encountered in the diet, ocelot, tapir and opossum (Table 1). The activity

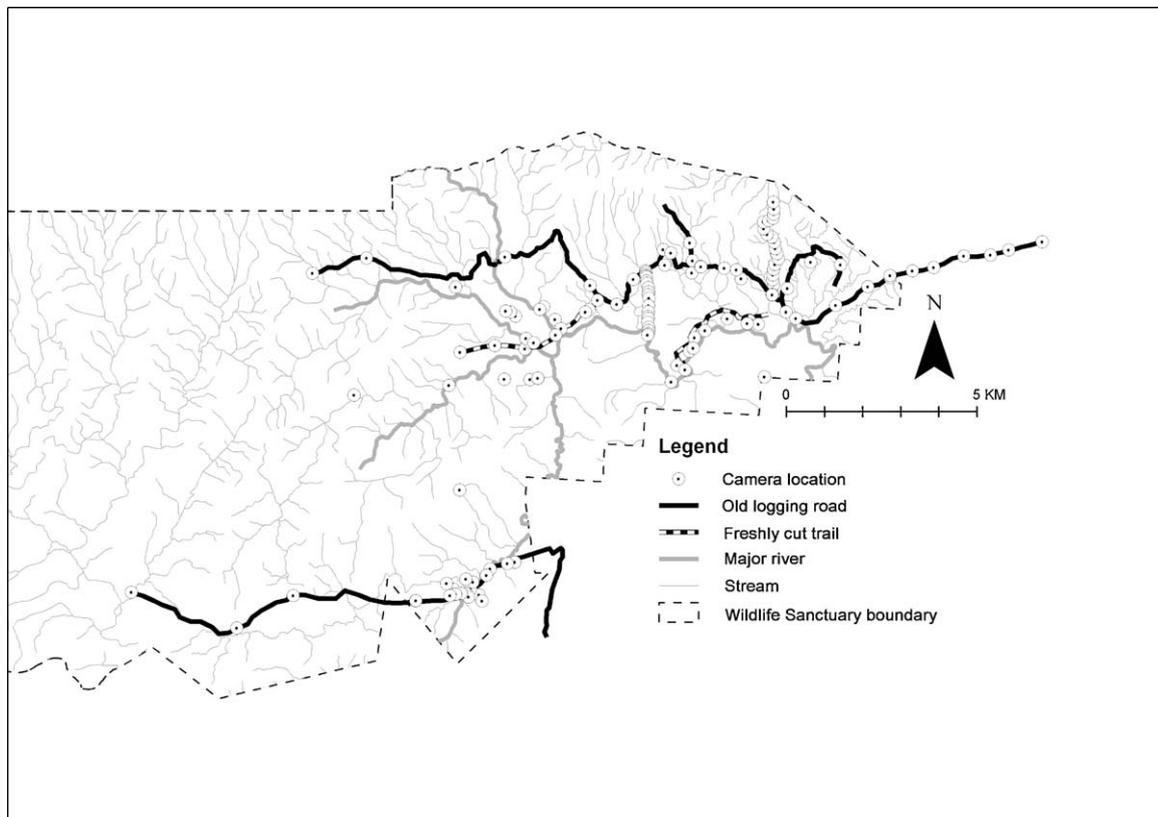


Fig. 1. Location of camera stations in the study area. Trails and waterways are shown.

pattern of ocelots was closely correlated with activity of both larger cats, while the activity of opossums was associated only with puma activity.

Moon phase and activity

Armadillos and pacas were the only prey species whose activity varied with moon phase. Percent capture success decreased significantly with moon phase for both species, indicating increased above-ground activity on darker nights (Fig. 3). Paca activity declined by a factor of 30 as the moon changed from new moon to full moon. The linear relation for armadillo was markedly lower compared to paca with only a small percentage (22%) of the variance explained by moon phase. However Fig. 3 indicates that armadillo activity also declined as the moon became brighter, with activity stable until 4 days before full moon followed by a marked drop-off in activity. No decline in activity was observed for the other nocturnal, control species: common opossums, tapirs and ocelots.

Across all locations, neither jaguar nor puma activity varied with moon phase (Fig. 3). Nor was there evidence that diurnal activity of jaguars or pumas increased during full moons when armadillo

and paca activity declined ($p > 0.1$). However at locations with frequent armadillo captures, jaguars were most active on dark nights, their activity increasing by 50% between full moon and new moon (Fig. 4). The relation could only weakly be described as linear with a mere 22% of the variance explained. No such pattern was detected between puma activity and moon phase at locations associated with high paca activity.

Discussion

Activity patterns of jaguars vary considerably within and between study sites. They are primarily nocturnal in the Venezuelan llanos (Scognamillo et al., 2003), the dry forests of Mexico (Núñez et al., 2002), and the Belizean rainforest (Rabinowitz and Nottingham, 1986; Harmsen et al., 2009); they show crepuscular activity peaks in the Bolivian Chaco (Maffei et al., 2004). They are most active during the day in Brazilian Pantanal (Crawshaw and Quigley, 1991), whilst in the Peruvian Amazon jaguars are equally active day and night (Emmons, 1987). Studies that collected data on both jaguars and pumas have found overlapping activity patterns in both species (Núñez et al., 2002; Scognamillo et al., 2003; Harmsen et al., 2009).

In this study, activity of jaguars and pumas coincided with periods when their main prey species forage above ground, as has been found for feline predators of rodents and lagomorphs (e.g. Fedriana et al., 1999; Roth and Lima, 2007). In other parts of the neotropics, jaguars and pumas rely more on diurnal ungulate species as prey (e.g. Crawshaw and Quigley, 2002; Núñez et al., 2000; Scognamillo et al., 2003; Taber et al., 1997). For example, in the Pantanal jaguars are mostly diurnal and feed mainly on domestic and wild ungulates, and capybaras (*Hydrochaeris hydrochaeris*) (Crawshaw and Quigley, 1991, 2002). In Venezuela, jaguars and pumas were active for 30–50% of the daylight hours compared to 40–60% during the

Table 1

Pearson correlations between 24-h activity patterns of jaguars or pumas and prey and control species. Significant correlations ($p < 0.05$) are shown in bold.

Species	Jaguar	Puma
Armadillo (main prey of jaguar)	0.33	0.36
Paca (main prey of puma)	0.43	0.51
Ocelot (control)	0.76	0.75
Tapir (control)	0.64	0.65
Opossum (control)	0.29	0.52
Brocket deer (prey)	−0.30	−0.32
Collared peccary (prey)	− 0.69	− 0.61
White-lipped peccary (prey)	−0.36	− 0.50

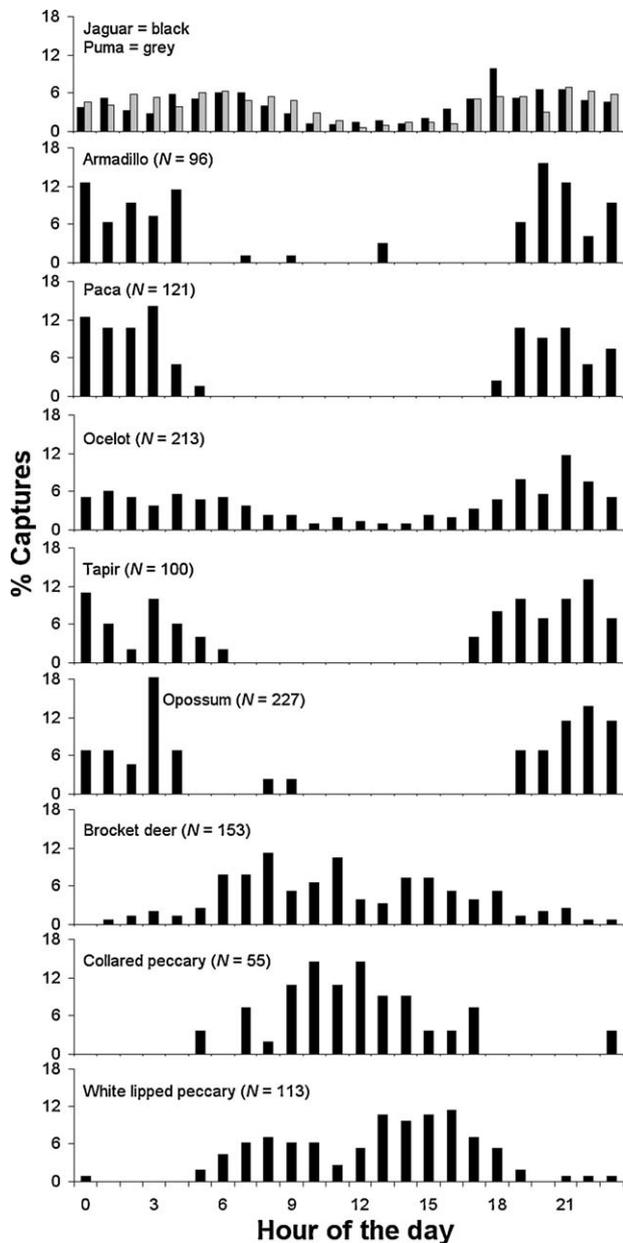


Fig. 2. Activity patterns of jaguar, puma, prey species and control species (N = number of captures).

night-time hours (Scognamillo et al., 2003). There, jaguars consumed mainly capybaras and peccaries (*Tayassu* sp.) and pumas mainly consumed livestock and collared peccaries (*Tayassu tajacu*) (Polisar et al., 2003). In contrast, in CBWS, 70% of jaguar and puma activity occurred at night and only 30% during daytime hours. Here, the nocturnal activity patterns of jaguars and pumas did not fully overlap with the two main prey species, indicating they also allocate activity to periods when other important prey species are active. White-lipped peccaries and red brocket deer are second most important prey in jaguar and puma diets respectively (Foster et al., 2010). Jaguar activity showed a crepuscular peak between 18:00 and 19:00, a period when white-lipped peccaries were still active, while pumas remained active for longer during the morning than did jaguars, a period when red brocket deer are active.

The nocturnal behaviour of armadillos and pacas could be an adaptation to predation risk, especially for pacas whose vegetarian diet (Reid, 1997) should otherwise allow them to forage at any time.

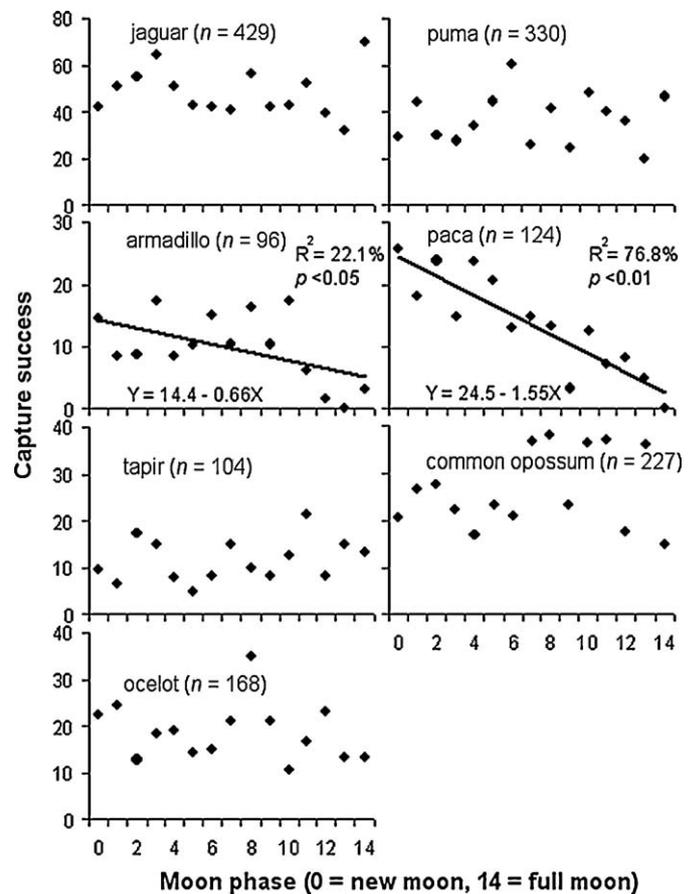


Fig. 3. Variation in capture success (activity) of nocturnal species with moon phase. The capture success during each of the 15 moon phases were corrected for the frequency of each phase in the total sampling period with 31 new moon and 30 full moon events sampled and ~60 events sampled for all other moon phase events (range 56–63). N indicates the sample size of captures with known moon phase used for the analysis.

Armadillos feed on arthropods (Reid, 1997) and so optimal foraging may reflect a trade-off between foraging during periods of high invertebrate availability and minimising vulnerability to predators. Both prey species appear to further reduce predation risk by lowering their activity during bright moonlit nights, as has been observed in many smaller rodent species (e.g. Daly et al., 1992; Lockard and Owings, 1974; Kotler et al., 2004; Wolfe and Summerlin, 1989). This is likely a strategy to avoid jaguars and pumas since the activity patterns of nocturnal non-prey species, ocelots, tapirs and opossums (a carnivore, herbivore and omnivore respectively), did not covary with moon phase. In locations with more dense undergrowth where armadillos are common, jaguar activity declined with both increased moonlight and reduced armadillo activity. Thus jaguars seem to respond to the lowered availability of armadillos during

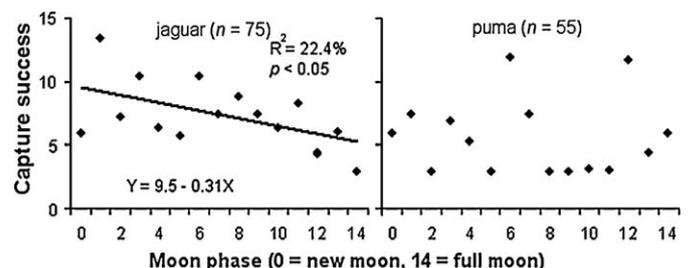


Fig. 4. Activity responses to moon phase by jaguars and pumas on locations with ≥ 2 captures/100 days of pacas and/or armadillos. Measurements as in Fig. 2.

bright nights by lessened activity in areas where armadillos are usually common. This contrasts with the behaviour of ocelots in Peru, which respond to brighter moonlight with increased activity in the more covered forest patches (Emmons et al., 1989).

Unlike jaguars, puma activity did not vary with the level of moonlight, even though their main prey species, pacas, responded more strongly to moon phase than armadillos. There was no evidence that pumas compensated for lowered availability of their main prey on bright nights by increasing their activity. Neither cat species compensated for decreased availability of their main prey by increasing their daytime activity which could otherwise facilitate hunting of diurnal prey. It is however likely that both jaguars and pumas do compensate by altering their hunting grounds and activity patterns to coincide with the availability of alternate prey assemblages during bright moonlit nights. In the Brazilian Amazon it has been suggested that jaguars and pumas track their main prey (Mendes-Pontes and Chivers, 2007).

Diet differentiation seems to be an important mechanism facilitating the coexistence of jaguars and pumas in the CBWS (Harmsen et al., 2009; Foster et al., 2010). Unravelling what drives this process requires a better understanding of hunting behaviour and predator avoidance. Further study quantifying light availability per location, taking into account cloud cover would be beneficial. Although camera-trap data can provide useful data on many individuals (e.g. Harmsen et al., 2009), telemetry data are needed for a more detailed insight into the hunting strategies of jaguars and pumas and predator-avoidance behaviour of their prey.

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