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Puma activity patterns and temporal overlap with prey in a human-modified landscape at Southeastern Brazil

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Abstract

Animal activity patterns correspond to the individual diel cycle time and is an important attribute of species coexistence in ecological communities. However, activity patterns of most Neotropical species are still poorly understood. Based on an 8-year camera-trapping survey conducted between 2009 and 2017, we evaluated puma (*Puma concolor*) activity patterns in a human-modified landscape in Southeastern Brazil. Our objectives were to determine the activity pattern of pumas and to verify the influence of main prey species and anthropogenic factors on their behavior. We categorized activity patterns of all assessed species based on the proportion of independent records during night and day times. We tested for sex differences in activity patterns of pumas, and measured their overlap with most consumed prey, people, cattle and domestic dogs. Our results suggested that males engaged in mostly nocturnal behavior while females were active both at night and day hours. Pumas exhibited higher coefficient of overlapping with prey species that were most often included in their diet, suggesting that prey availability might influence puma activity or that pumas opportunistically prey upon species with similar activity pattern. Female pumas seem to be more exposed to anthropogenic threats due to higher activity pattern overlap with people and domestic dogs. Our findings provide insights into puma-prey temporal behavior, highlighting the relevance of intrasexual dissimilarity in the activity patterns of a top predator living in a disturbed landscape.

Introduction

The activity patterns are an important attribute of a species behavior and correspond to its individual biological rhythms. Species activity patterns are shaped by different factors, such as physiological adaptations, abiotic conditions (Nielsen, 1984; Scheibe *et al.*, 1999) and species life strategies (e.g. social organization, avoidance of competitors) (Gittleman & Harvey, 1982). In addition, access to important resources, particularly prey, play a strong role in determining carnivores species' daily cycles (Brown *et al.*, 2001). Some predators are known to locally adjust their foraging period to align with the activity of their main prey, thus optimizing energy gain (Karanth & Sunquist, 2000; Foster *et al.*, 2013). For instance, although jaguars (*Panthera onca*) are considered generalist predators and mostly nocturnal across different biomes, in habitats with high availability of diurnal prey, jaguars may show diurnal peaks (Crawshaw & Quigley, 1991; Foster *et al.*, 2013). The same behavior has been reported for African leopards (*Panthera pardus*), which are mostly nocturnal in savannah environments, but mainly diurnal in rainforests, as is their main prey in this type of habitat (Jenny & Zuberbühler, 2005).

More recently, it has been reported that some levels of human-driven disturbances and anthropogenic related activities (e.g. settlements, roadways, presence of domestic animals and persecution) might influence carnivores activity patterns (Ngoprasert, Lynam & Gale, 2007). Pumas (*Puma concolor*) and bobcats (*Lynx rufus*) may shift their activity patterns to avoid encounters with people, leading to altered competitive interactions between the two predators (Lewis *et al.*, 2015). Likewise, leopards may alter their temporal activity pattern in response to high human pressure within and outside protected areas (Ngoprasert *et al.*, 2007; Carter *et al.*, 2015).

Although some studies have investigated carnivores activity patterns in South America, most of them were carried out inside protected areas (Gómez *et al.*, 2005; Di Bitetti *et al.*, 2009, 2010; Harmsen *et al.*, 2009, 2011; Romero-Muñoz *et al.*, 2010; Blake *et al.*, 2012; Massara *et al.*, 2016; Porfirio *et al.*, 2016, 2017). Few information is available in non-protected landscapes or assessing effects of anthropogenic factors on species biological rhythms in Neotropical regions (Scognamillo *et al.*, 2003; Paviolo *et al.*, 2009; Kolowski & Alonso, 2010; Foster *et al.*, 2013).

South American pumas were described as primarily crepuscular-nocturnal (Hornocker & Negri, 2010), although a cathemeral behavior, that is, activity distributed approximately evenly throughout the 24 h of the daily cycle (van Schaik & Griffiths, 1996), was registered for the species (Gómez *et al.*, 2005; Di Bitetti *et al.*, 2010; Romero-Muñoz *et al.*, 2010). Notwithstanding, no differences in daytime use among sexes have been reported (Romero-Muñoz *et al.*, 2010). The objectives of this study were to describe the activity patterns of pumas and to investigate factors that may influence the species behavior in a human-modified landscape at Southeastern Brazil. We focused on three main questions: (1) Is there a difference between male and female temporal activity patterns? (2) How do puma activity patterns overlap with those of their main prey species? (3) How do puma activity patterns overlap with those of people, cattle (*Bos taurus*) and domestic dogs (*Canis lupus familiaris*)? We hypothesized that there would be no difference in activity pattern between male and female pumas, as to our knowledge it has never been documented before. Specifically, we predicted that (1) both sexes would be active at the same time during a 24-h period; (2) there would be high activity overlap between pumas and their main prey species; and (3) there would be low activity overlap between pumas and people, cattle and domestic dogs.

Materials and methods

Study site

This research was conducted in Minas Gerais State, at the *Triângulo Mineiro* region, municipality of Araguari, Brazil (18°46′S, 48°14′W and 18°21′S, 48°38′W; Fig. 1), an ecotone zone within Cerrado and Atlantic Forest biomes (Lopes *et al.*, 2012). Currently, the area comprises highly fragmented landscape represented by a matrix of multiple land uses dominated by cattle ranches with exotic pasture grasses (mainly *Urochloa* sp.), agriculture and human habitations. Different anthropogenic pressures, such as the presence of people, livestock and domestic dogs in natural habitat patches are constant in the study site. Remaining natural vegetation is restricted to scattered patches of savannah and mesophytic seasonal forest (*sensu* Oliveira-Filho & Ratter, 2002) which are mainly concentrated along the margins of the Araguari and Paranaíba rivers and their tributaries. Most of the extensive vegetation removal in the study area occurred in the late 1970s and natural habitat remains has suffered minimal reduction since then.

The regional climate is marked by two distinct seasons, one hot and wet from October to April and another cold and dry from May to September (Alvares *et al.*, 2013). Mean annual temperature and precipitation vary between 22–25°C and 1600–1800 mm, respectively (data available at CPTEC/INPE).

Camera-trapping

This study is part of a long-term research project on pumas ecology focused on developing regional conservation strategies for a non-protected area in Southeastern Brazil. To

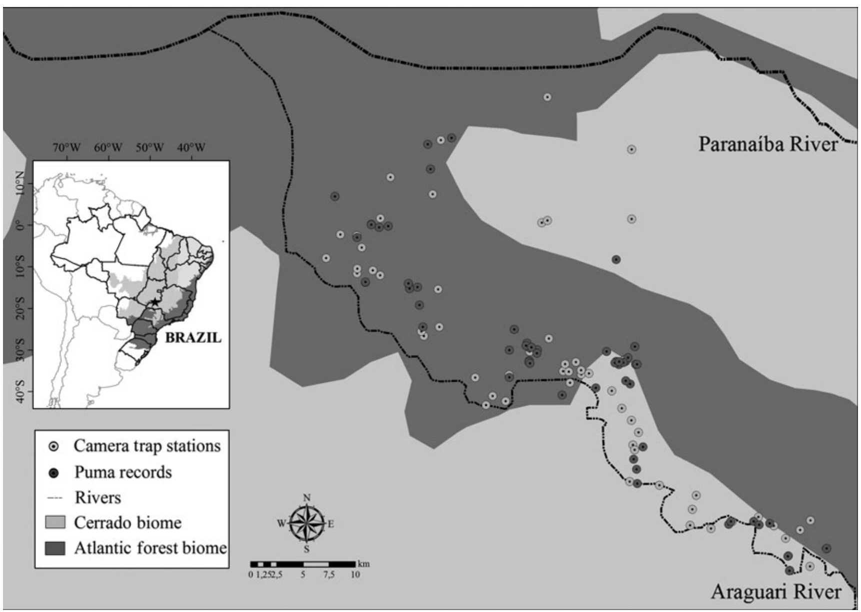

Figure 1 Location of study site and map of camera stations installed between 2009 and 2017 in the municipality of Araguari, *Triângulo Mineiro* region, Minas Gerais state, Brazil.

investigate the activity patterns and temporal overlap between pumas, their main prey and anthropogenic factors, we selected camera-trap records obtained during camera-trapping surveys carried out to identify suitable sites for capturing pumas. To maximize the opportunity to detect pumas we prioritized game trails, abandoned roads, or human paths as locations for camera stations (Srbek-araujo & Chiarello, 2013). In total 117 different camera stations were deployed ($\bar{X}$ = 26.42 ± 7.44 SD cameras per year) between January 2009 and August 2017 encompassing a sampled area of approximately 300 km^2 (Fig. 1). Camera-traps were placed at irregular intervals ranging from 0.3 to 8.0 km ($\bar{X}$ = 1.9 km) from each other, with a sampling effort varying from six to twelve months per year. Each camera station consisted of one or two independent camera-traps (Tigrinus©, Santa Catarina, Brazil; and Bushnell©, Kansas, USA models) set to take photos or videos with an interval of 30 s between records. Camera-traps were checked approximately every 20 days. By pooling together records from multiple years, we assumed that species detection and activity patterns were similar across years. Camera-trap surveys were carried out in exactly same region during consecutive years and we are not aware of any significant biological, environmental or anthropogenic changes in the area during the study time.

Prey species

We confirmed puma main prey species in the study site using ancillary puma feeding habits data obtained through visits to clusters of locations (*n* = 130) of six puma (four males and two females) equipped with Global Position System (GPS) radio-collars (Lotek® Fish & Wildlife Monitoring, Ontario, Canada/44400S and 4550S models; and Sirtrack® Wildlife Track Solutions, Hawkes Bay, New Zealand/G5C 375B Pinnacle Iridium model) monitored between February 2012 and November 2017. Clusters of locations were defined as any three or more locations within 50 m of each other elapsed over a minimum of 24 h (adapted from [Anderson & Lindzey, 2003;]). We determined consumed species found at the visited cluster of locations by identifying carcasses or prey remains (i.e. hair, skin, feather and bone fragment) to the smallest taxonomic group possible. Pumas' prey species registered in the study site were listed in the Table S1, being capybara (*Hydrochoerus hydrochaeris*), giant anteater (*Myrmecophaga tridactyla*), tegu lizard (*Salvator merianae*), armadillos (nine-banded [*Dasypus novemcinctus*] and six-banded [*Euphractus sexcinctus*]), and common opossum (*Didelphis albiventris*) the most important prey; pumas also preyed upon livestock, such as cattle – *B. taurus* and horses – *Equus caballus*.

For all fieldwork, we followed guidelines approved by the American Society of Mammalogists (Sikes & Gannon, 2011), by the Brazilian government (Instituto Chico Mendes de Conservação da Biodiversidade/SISBIO, license number 14576-6/2009 – 2015), by the Ethics Committees on Animal Use of Universidade Federal de Viçosa (process number 90/2014) and Universidade Federal de Goiás (process number 066/2014).

Data analysis

For each camera-trap record, we identified the species, date, time and camera station. We defined multiple records of the same species at the same camera station as independent when pictures were taken at least 30 min apart, unless we were able to unambiguously identify different individuals (Linkie & Ridout, 2011). Because more than one camera station could be located along the same road or trail, to avoid spatial pseudoreplication, we also considered it to be a single record when the same species or individual was photographed in two or more neighboring camera stations within a 30-min interval. Any camera station placed less than 400 m apart were considered neighbors and consecutive records at neighboring cameras were excluded from the dataset (Ridout & Linkie, 2009). Records of multiple individuals of social species, such as collared-peccaries (*Pecari tajacu*), coatis (*Nasua nasua*), capybaras, livestock and domestic dogs, were considered to be a single record of the species.

Activity patterns were based on the proportion of independent records during the night (from sunset to sunrise) and day (from sunrise to sunset), following van Schaik & Griffiths (1996). Species were classified as diurnal (<10% of records at night), nocturnal (≥90% of records at night), mostly diurnal (10–29% of records at night), mostly nocturnal (70–89% of records at night), or cathemeral (30–69% of records at night) (Gómez *et al.*, 2005). To account for the successive changes of sun's position throughout the year in the celestial sphere (Nouvellet *et al.*, 2012), prior to analysis we adjusted each record to the specific day sunrise time (or sunset time if night record) and then we adjusted sunrise and sunset to $\pi/2$ and $3\pi/2$, respectively.

We used the method developed by Ridout & Linkie (2009) to determine daily activity pattern of each species and measure the overlap between pumas, prey and anthropogenic factors (people, cattle and domestic dog). First, a non-parametric circular kernel-density function was employed to assess daily activity patterns. Second, a coefficient of overlapping (Δ), were used to measure the extend overlap between two kernel-density estimates, taking the minimum of the density functions from two set of samples being compared at each point in time. Overlap was assumed as the area lying under both of the density curves. The coefficient of overlapping ranged from 0 (no overlap) to 1 (complete overlap) (Ridout & Linkie, 2009; Linkie & Ridout, 2011). We used Δ_4 for large samples (>75 camera records) otherwise we used Δ_1 as suggested by Meredith & Ridout (2016). We calculated the 95% confidence intervals of each overlap index using smoothed bootstrap with 10 000 resamples (Meredith & Ridout, 2016). All analyses were performed in R environment v.2.6 (R Development Core Team 2014) using the 'overlap' R-package (Meredith & Ridout, 2016). Some consumed prey species were not registered by camera-traps or were recorded in low numbers (i.e. common opossum, six-banded armadillo and domestic fowl), hence not allowing for temporal analyses.

We conducted a simple comparison between group means using generalized linear models (GLM) to test if the mean number of records per hour of pumas differed between day and night hours. The groups are 'night hours' and 'day hours'. Therefore, our sampling unit is every hour. Hours between sunrise and sunset belong to the 'day hour' group, while hours between sunset and sunrise, 'night hour' group. We used a quasi-Poisson distribution to account for overdispersion in the count data (records per hour) (Breslow, 1990). We tested male and female pumas separately to allow us to detect differences in activity patterns in relation to gender.

Results

Across 8 years of camera-trapping, we obtained 2667 independent activity records, including pumas (n = 472; 275 registers for males, 63 for females and 134 unidentified; Fig. S1), prey species (n = 1329 records; Fig. S2), cattle (n = 409), domestic dogs (n = 250 records), and people (n = 207 records). Pumas were registered at 63 of the 117 camera stations. We were able to uniquely identify at least 20 animals (10 males and 10 females). Pumas were active mostly during nighttime (72.5% of records; Table S2) and, in general, activity had a peak in the middle of night, declined after 04:00 h, and reached lowest percentages around noon.

Male and female pumas presented dissimilar activity patterns (Fig. 2). The mean number of male records per hour during night hours was significantly higher than during day hours (z = 5.56, d.f. = 23, P = <0.001), showing they are mostly nocturnal (77.8% of male records occurred during night period). However, we found no significant difference in the mean number of records of females between night and day hours (z = 0.371, d.f. = 23, P = 0.71), indicating more cathemeral behavior for females. Males showed two peaks of high activity, one after the beginning of night and another right before sunrise. Although females also had a peak of activity before sunrise, they had activity peaks in the morning and afternoon (when males were mostly inactive) and kept their activity relatively low while males exhibited increased activity after sunset.

Male and female pumas exhibited different coefficients of overlapping with main prey species (Table 1). Male pumas had a high overlap with their most consumed items: capybaras (Δ = 0.85), giant anteater (Δ = 0.81) and nine-banded armadillo (Δ = 0.76) (Table 1). Female pumas overlapped less than

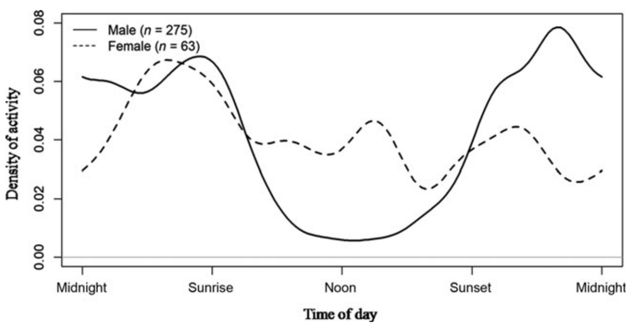

Figure 2 Activity pattern of male (n = 275) and female (n = 63) pumas (*Puma concolor*) based on camera-trap surveys (from 2009 to 2017) in the municipality of Araguari, Minas Gerais state, Brazil.

males with prey in general and their most consumed prey were not the one with highest overlap. However, temporal overlapping of females and diurnal prey, such as coatis and tegu lizard (which are often consumed by females), were higher than for males (Fig. S3). Graphical representation of prey species overlap with males and females can be found in Figs. 3 and 4, respectively.

Male pumas tended to overlap significantly less with people, domestic dogs and cattle than females (Fig. S3). With respect to temporal overlap, female pumas had a higher overlap with people and domestic dogs. Graphical representation of the overlap of anthropogenic factors (people, cattle and domestic dog) with males and females can be found in Fig. 5.

Discussion

Due to their elusive habits, behavioral knowledge from Neotropical wild felids is still scarce in the literature, especially for those living within human-modified landscapes. Filling part of this gap, our study used both camera-trap and feeding habits information to show evidence that puma activity and diet can differ between sexes and consequently, with their main prey and possible disturbing agents (as anthropogenic factors). In general, we found that the difference in activity pattern for males and females corresponded to differences in most consumed items. Data also suggest females might be more exposed to interactions with anthropogenic factors.

Contrary to our first prediction, and also to what has been reported for pumas in other biomes (Romero-Muñoz *et al.*, 2010), the higher estimate of mean number of male records per hour at night suggested that males are significantly more nocturnal than females, which showed cathemeral behavior. Although our data do not allow inference of causality, the use of day hours by females could reflect a strategy to diminish encounters with males and/or increase encounters with diurnal prey. Spatial segregation has been suggested when females avoid male-dominated travel routes because such encounters may result in agonistic events (Harmsen *et al.*, 2009). For instance, in New Mexico, males accounted for 53% of the death causes for monitored females and their cubs (Logan & Sweanor, 2001). Results of spatial overlapping studies revealed that pumas rarely associate, and most male-female interactions were related to courtship (Logan & Sweanor, 2001). If spatial avoidance behavior happens in puma interactions, temporal avoidance is also a possible mechanism to increase female puma's survival and fitness.

Besides intraspecific interactions, several studies have related species activity patterns to prey availability (Di Bitetti *et al.*, 2010; Harmsen *et al.*, 2011; Foster *et al.*, 2013; Ross *et al.*, 2013). Among carnivores, synchronized activity between predators and prey may represent an optimization of foraging time to maximize energetic gain (Brown *et al.*, 2001). Savanna ecosystems in subtropical regions are known for their species-rich wildlife that occupy different niches in complex communities (Paglia *et al.*, 2012). Therefore, the great variety of available prey (Oliveira & Marquis, 2002) offers an array of food items that can be consumed at alternative periods of the day. Cathemeral behavior increases probability of encounters

Table 1 Number of independent camera-trap records (*n*), classification of daily activity patterns, estimates of coefficients of overlapping (Δ) of wild prey species with pumas (*Puma concolor*) and 95% confidence intervals (CI). Data are from camera-trap survey in the municipality of Araguari, Minas Gerais state, Brazil, from 2009 to 2017

		Puma concolor			
		Male (*n* = 275)		Female (*n* = 63)	
Species	*n*	Estimate	CI	Estimate	CI
Prey					
Myrmecophaga tridactyla	626	0.81	0.74–0.86	0.61	0.49–0.71
Pecari tajacu	451	0.81	0.74–0.86	0.73	0.62–0.83
Sylvilagus brasiliensis	79	0.81	0.71–0.88	0.57	0.45–0.68
Nasua nasua	59	0.26	0.18–0.34	0.48	0.35–0.60
Dasypus novemcinctus	48	0.76	0.64–0.85	0.57	0.43–0.70
Salvator merianae	45	0.14	0.06–0.21	0.35	0.22–0.47
Hydrochoerus hydrochaeris	21	0.85	0.68–0.96	0.69	0.50–0.85
Anthropogenic factors					
Bos taurus	409	0.27	0.22–0.32	0.50	0.39–0.61
Canis lupus familiaris	250	0.48	0.40–0.54	0.67	0.55–0.77
People	207	0.39	0.33–0.45	0.57	0.45–0.67

with a more diverse prey base (Scognamillo *et al.*, 2003). This might be beneficial to a generalist carnivore, as the puma, which may consume a broad variety of prey including diurnal and nocturnal species (Murphy & Ruth, 2010). Diurnal habits of females may be related to their more diversified diet in relation to males. This hypothesis is supported by our results. While three main prey constitute the base of the diet of males, females preyed upon different species with more similar frequencies, having as main prey both diurnal (tegu lizard) and nocturnal (nine-banded armadillo) species.

The overlap between pumas and collared-peccaries deserves further comments. This is the second most recorded prey species in our camera-trap survey. However, it corresponded to less than 3% of consumed items. This low frequency of collared-peccary is an exception in the literature, being usually reported as one of the main prey for pumas in other areas (Martins, Quadros & Mazzolli, 2008; Murphy & Ruth, 2010). It would be expected that collared-peccaries should be more often consumed by pumas in general, which have high temporal overlap with the species. However, peccaries live in alert groups and may show defensive strategies and aggressive behavior towards predators (Taber *et al.*, 2011), making them a less appealing food resource due to the risk of injury, particularly to female pumas (considerably smaller than males in our study site).

People, livestock, domestic dog and pumas were often photographed in the same camera-trap stations. Although private remnants of natural vegetation (where camera-traps were placed) are protected by the Brazilian environment law, they are used by people as access to local rivers for fishing and recreation. They are also used illegally for raising livestock and hunting. In general, people, cattle and domestic dogs were more active during daylight hours, leading to a higher overlap with female pumas than with males. Cattle could be perceived by pumas as either a food resource or as an anthropogenic disturbance factor. Our results showed low overall activity overlap between pumas and cattle and also low frequency of cattle on puma's diet, suggesting cattle may act more as a disturbing agent than as a food resource. The fact that pumas are not preying on cattle, but instead consuming mainly wildlife, is an important aspect and may be considered as a tool for regional puma conservation, as retaliation killing is one of the main causes of puma mortality in different parts of Brazil (Azevedo *et al.*, 2013b). However, the fact that females are more exposed to encounters with people and domestic dog can represent higher mortality risk. Humans are among the major causes of death in most puma populations (Logan & Sweanor, 2001). This is a concern because females are important for population long-term viability, once their survival has a strong impact on the number of youngs produced (Lindzey *et al.*, 1992; Logan & Sweanor, 2001; Lambert *et al.*, 2006).

Our study used camera-trapping, GPS radio-collar technology and diet information to obtain novel insights into how puma behavior can differ between sexes. However, our study has caveats that often affect non-systematic data collection. For the activity pattern analysis, we pooled together data from 8 years. Therefore, we concede there might be seasonal and inter-annual noise in our data. Even though our dataset is one of the largest puma information available for non-protected areas, the sample sizes, particularly for female pumas and some prey species, do not allow annual or seasonal analyses. This is an inherent problem in studies focused on species with elusive behavior, large home-ranges and/or naturally low densities, such as pumas in our study area. Despite the seasonal and annual noise that our data may have, we were able to detect some interesting signals on how male and females differ in their use of time. Another issue is related to the female puma's diet, which was characterized using data from two individuals. Trapping large-bodied wild cats is remarkably difficult, particularly in human-dominated landscapes, where species are adapted to avoid people. Our study reports data on the first pumas monitored by GPS radio-collars in Brazilian savanna non-protected areas (Azevedo *et al.*, 2013a) and considering the low density puma population in our study site, six

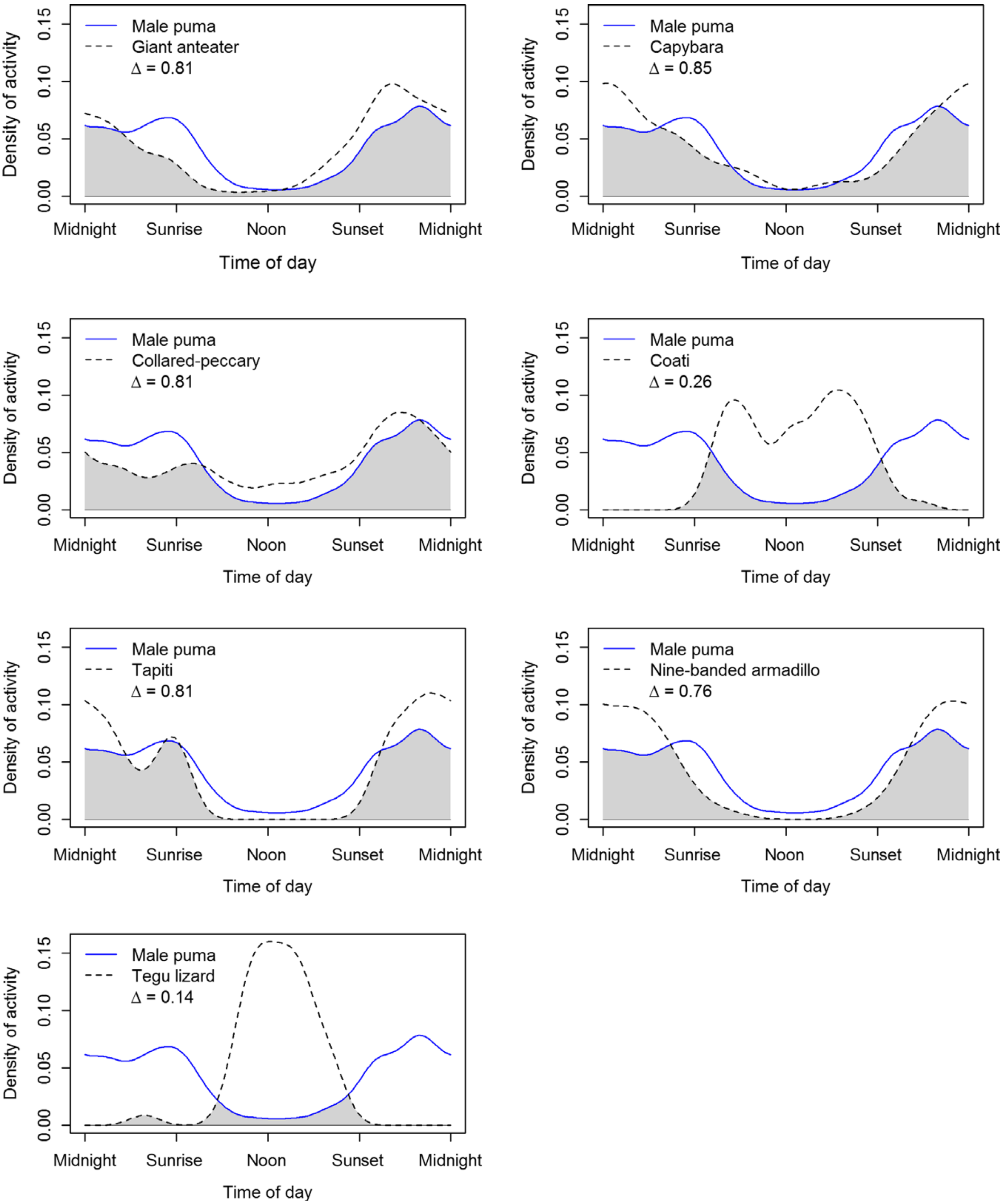

Figure 3 Density estimates of daily activity patterns of male pumas (*Puma concolor*) and main prey in the municipality of Araguari, Minas Gerais state, Brazil. Solid lines are kernel-density estimates for pumas, whereas dashed lines are prey species. The coefficient of overlapping is represented by the shaded area. [Colour figure can be viewed at zslpublications.onlinelibrary.wiley.com]

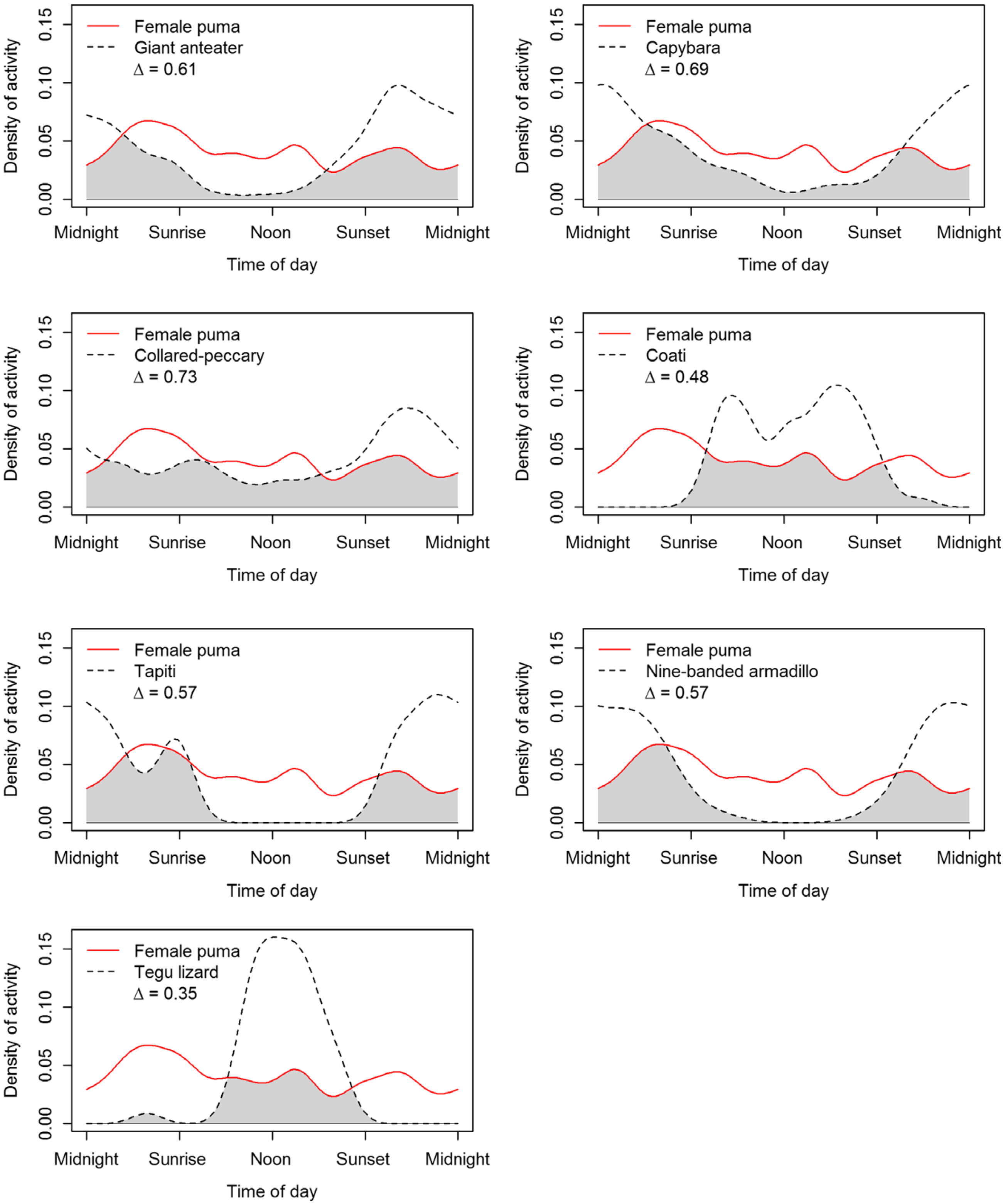

Figure 4 Density estimates of daily activity patterns of female pumas (*Puma concolor*) and main prey species in the municipality of Araguari, Minas Gerais state, Brazil. Solid lines are kernel-density estimates for pumas, whereas dashed lines are prey species. The overlapping coefficient is represented by the shaded area. [Colour figure can be viewed at zslpublications.onlinelibrary.wiley.com]

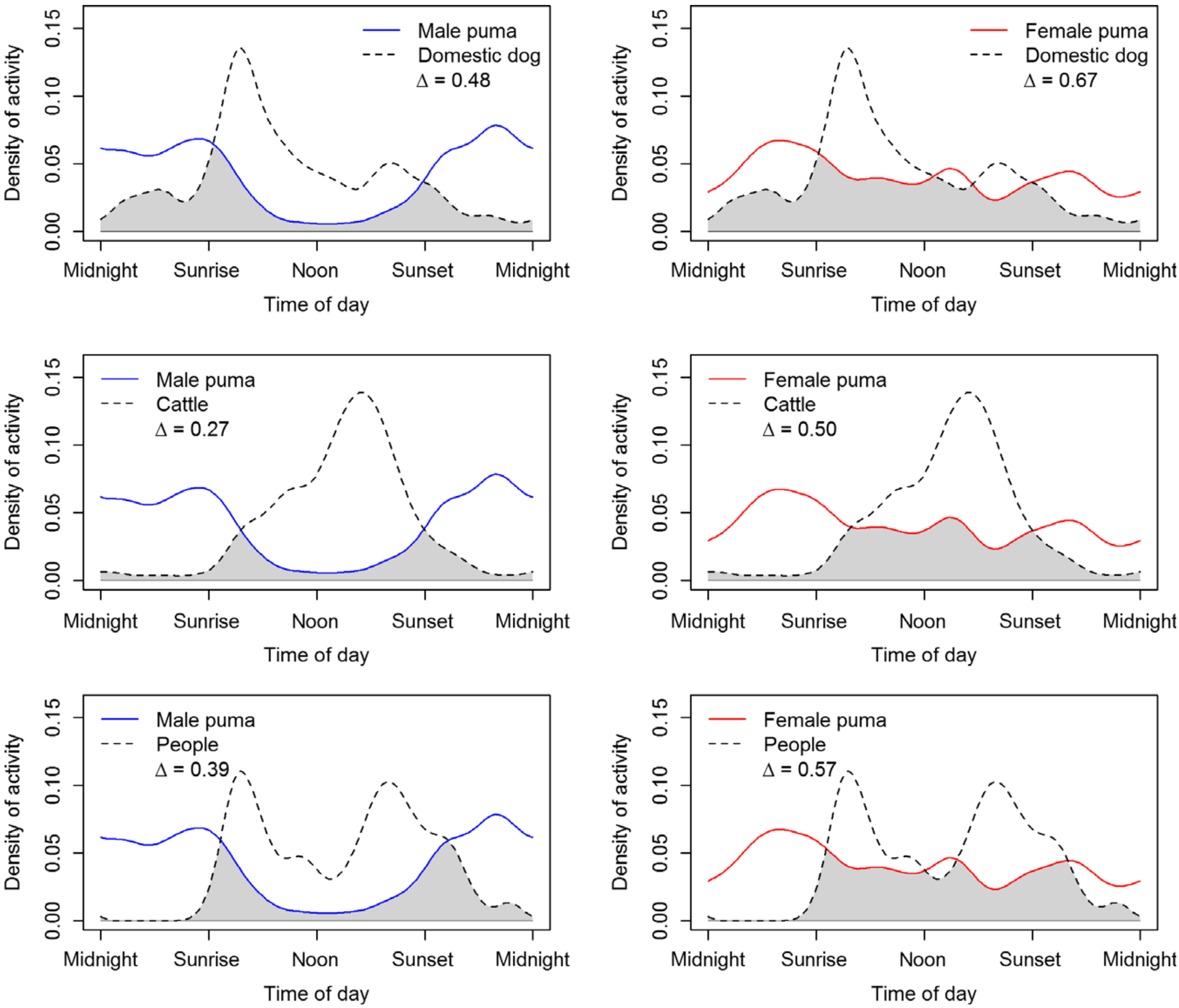

Figure 5 Density estimates of daily activity patterns of male and female pumas (*Puma concolor*) and anthropogenic factors: domestic dog (*Canis lupus familiaris*) cattle (*Bos taurus*) and people in the municipality of Araguari, Minas Gerais state, Brazil. Solid lines are kernel-density estimates for pumas, whereas dashed lines are species that represent anthropogenic disturbances. The overlapping coefficient is represented by the shaded area. [Colour figure can be viewed at zslpublications.onlinelibrary.wiley.com]

individuals are probably quite representative of the entire local population.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Figure S1. Pumas (*Puma concolor*) registered at camera-trap survey between 2009 and 2017 in the municipality of Araguari, Minas Gerais state, Brazil.

Figure S2. Prey species registered at camera-trap between 2009 and 2017 in the municipality of Araguari, Minas Gerais state, Brazil.

Figure S3. Estimate overlap index and 95% of confidence interval (CI), for pumas (male and female separately) and wild prey species and anthropogenic factors (domestic dog, cattle, and people), registered at camera-traps between 2009 and 2017 in the municipality of Araguari, Minas Gerais state, Brazil.

Table S1. Prey species consumed by pumas (*Puma concolor*) at Araguari, Minas Gerais state, Brazil. Species diet was assessed through visiting clusters of locations (n) of monitored pumas ($n = 6$).

Table S2. Activity patterns classification (based on % of camera-trap records) of pumas (*Puma concolor*) and prey species in the Municipality of Araguari, Minas Gerais state, Brazil.