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Effect of sex, age, and reproductive status on daily activity levels and activity patterns in jaguars (*Panthera onca*)

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Abstract

All animals, including carnivores, adapt their daily activity duration and distribution to satisfy food demands, breed, or avoid mortality risk. We used the kernel density method to estimate daily movement activity levels and movement activity patterns of jaguars in Hato Piñero, in Venezuelan Western Llanos, based on 3,656 jaguar detection time records from two and a half years of camera trapping. Jaguars were active for 11.7 h per day on average and exhibited mostly nocturnal and crepuscular activity pattern, however, with marked differences between sex/age/reproductive groups. Reproductive females had the highest daily activity level (13.2 h/day), followed by adult males (10.9 h/day), non-reproductive females (10.5 h/day), and cubs (8.7 h/day). Activity patterns also differed, with males and reproductive females having activity peaks at the same hours after sunset and before sunrise, cubs in the night and after sunrise, while non-reproductive females were most active during night hours. This study was the first to document the effect of sex, age, and reproductive status on daily level and activity pattern in the jaguar.

Keywords Circadian activity · Felid ecology · Hato Piñero · Large cats · Mammal ethology · Movement activity

Introduction

All animals, including carnivores, split their time between various life activities and resting or sleeping. The time length during the day when they stay active (hereafter "activity level") depends on the trade-off between their physiological needs and constraints and opportunities to meet various life needs, e.g., to satisfy food demands or to breed (Halle and Stenseth 2000). In carnivores in particular, the daily activity level may be shaped by prey availability (Zielinski 1988, 2000; Jędrzejewski et al. 2000). Distribution of time periods when animals stay active along the 24 h of day (hereafter "activity pattern") may also vary between species or individuals and may result from adaptations/limitations in their vision abilities, diurnal changes in food availability, interference from competitors, predation or hunting risk, daily temperature fluctuations and needs for thermoregulation, or from social behavior (e.g., Dunstone and Sinclair 1978; Gittleman 1986; Jędrzejewski et al. 1993, 2000). Carnivores often have to adjust their activity pattern to that of their prey, often seeking periods of the highest vulnerability of prey (Curio 1976; Linkie and Ridout 2011; Yang et al. 2018; Nagy-Reis et al. 2019; Rasphone et al. 2020) and to human activity, avoiding people by adjusting their movements in time and space (Theuerkauf et al. 2003). Information on activity levels and activity patterns may be important to understand distribution of energy expenditures,

niche overlaps, hunting strategies, predator–prey relations, or other aspects of animal ecology (Powell et al. 1985; Zub et al. 2009, 2013; Kemna et al. 2020; Mwampeta et al. 2020; Rasphone et al. 2020).

Large felids present complex behaviors that may differ between age, sex, and individuals of different reproductive status, which in turn can lead to variation in activity levels and activity patterns. Since females of most felids are solitary and solely responsible for raising offspring, they have to devote a considerable amount of time for hunting, vigilance, and tending cubs (Powell and Leonard 1983; Eisenberg 1986; Schmidt 1998). Adult males, apart from hunting for their own maintenance, constantly visit their large territories, assist their females and defend them against other males, and try to take over other females (Cavalcanti and Gese 2009; Morato et al. 2016; Kanda et al 2019). Subadult individuals have to disperse far to search their own territories. As infanticide is known from several large felids including jaguars (Loveridge et al. 2007; Barlow et al. 2009; Balme and Hunter 2013; Tortato et al. 2017), females and their cubs should be continuously alert and should avoid spatially and temporally any encounters with stranger males, which could result in different daily activity patterns. It has been shown that detectability and movement parameters obtained from camera trapping differ significantly between sex/age groups in jaguars (Jędrzejewski et al. 2017), suggesting likely differences in activity levels and activity patterns between sex/age groups.

The jaguar *Panthera onca*, being a representative of solitary felids, is a relevant model species for studying the intrinsic variation in the activity levels and activity patterns of these carnivores. Although previous studies have already provided data on the jaguar daily activity showing their prevailing nocturnal or crepuscular activity patterns, those studies were focused on competitive interactions with other large carnivore species and predatory relationships with their prey (Cavalcanti and Gese 2009; Romero-Muñoz et al. 2010; Harmsen et al. 2011; Foster et al. 2013; Porfirio et al. 2017; Herrera et al. 2018). Information on the intra-species variability in duration and circadian patterns of jaguar daily activity as well as the underlying factors are largely unknown.

In this paper, based on a large number of jaguar records from camera trapping, we estimate and compare levels and patterns of daily movement activity for four sex/age/reproductive groups of jaguars: adult males, adult reproductive females, subadult non-reproductive females, and cubs. We hypothesize that adult reproductive females should be active longer than non-reproductive ones due to their higher energetic demands and their activity pattern should be more diurnal as a result of maternal care, similarly as it was found in several other felids (Schmidt 1999; Manfredi et al. 2011; Martins and Harris 2013). We also predict that adult male jaguars should show a similar pattern as that of reproductive

females because much of their activity is related to acquiring access, assisting, or defending their females. We expect that the youngest cohort of jaguars will have the lowest activity level.

Study area

We conducted our study in Hato Piñero, Cojedes state, in Los Llanos of Venezuela. The area of Hato Piñero (800 km^2) includes the hills of the El Baúl range and the plains between the rivers Cojedes, Portuguesa, Chirgua, and Pao. The landscape is dominated by seasonally flooded lowland savannas, semi-deciduous dry forests, gallery forests, chaparrals, and pastures, all intersected by small rivers and canals. The climate has two seasons, a rainy season approximately between May and November and a dry season between December and April, with the mean of 1,500 mm of precipitation yearly. The relative impermeability of soil contributes to the floods that usually begin in June and have a maximum between July and August. Fires are common, and sometimes very intense, during the dry season. The study area has a rich natural fauna, typical for humid parts of Los Llanos (Polisar et al. 2003; Jędrzejewski et al. 2014, 2017). Until 2010, Hato Piñero was a private-owned ranch, that controlled hunting since 1951, and ran an ecotourism operation since 1980s. Now it is a state cattle ranch with some conservation regimes (no hunting, no forest exploitation, half of the area kept without cattle or any other human impact). Jaguars are protected inside Hato Piñero; however, they are commonly killed outside of its area. During the study period, the livestock herd was estimated at about 13,000 cattle, between 1,000 and 2,000 buffalos, and 200 horses.

Methods

Camera trapping

We conducted continuous camera trapping from July 2013 to February 2016 (935 days) in a 170 km^2 study area localized in the north-central part of the ranch (68.0334° W, 8.9827° N and 68.2148° W, 8.8562° N). We installed mostly HC 500 (Reconyx Inc., Holmen, WI, USA) and TrophyCam HD Max (Bushnell, Overland Park, MI, USA) cameras along dirt roads, rivers or streams, and animal paths with a general goal to fit a grid of 2 km × 2 km; however, we adjusted localization of cameras to the possibilities of camera installation and signs of jaguar presence (see Jędrzejewski et al. 2017 for a map of the spatial distribution of cameras, https://link.springer.com/article/10.1007/s13364-016-0300-2#Sec19). We visited the study area every 2–3 months, replacing batteries, memory cards and adjusting the position of cameras,

depending on actual conditions or records of jaguar tracks. The number of camera traps active at the same time varied from 27 to 56 (Jędrzejewski et al. 2017). Each station had a single camera trap tied to a tree at about 90 cm high and a bait that was a small piece of carpet soaked with beaver castoreum/catnip oil lure located 3 to 4 m away, in front of the camera (Schmidt and Kowalczyk 2006; Schlexer 2008). Such baits do not cause any important alteration of animal's behavior but they make that passing animals stop to sniff which improves the quality of pictures (Rovero et al. 2010; Jędrzejewski et al. 2017). We set the cameras to take pictures continuously (every 0.5 to 1 s, depending on camera type) when detecting animal movement, without any break or delay. The clock of each camera was set based on the solar time indicated by GPS Garmin 60C.

Data analysis

We identified individual jaguars based on spot patterns on the skin (Silver et al. 2004) and their sex, age, and reproductive state based on the presence/absence of testicles, nipples, and cubs. We distinguished four age/reproductive groups: adult males (M), adult reproductive females (RF), sub-adult non-reproductive females (NRF), and cubs (C) (Jędrzejewski et al. 2017). Cubs included apparently young, immature individuals that were recorded with an adult female. Females that were recorded with cubs or were recorded with signs of pregnancy or enlarged nipples indicating lactation were classified as reproductive. Females that were never recorded to have cubs and did not show any reproductive features were classified as sub-adult non-reproductive. Females that were first recorded as cubs, then as sub-adult females, then as reproductive females were classified respectively at each phase. We excluded from the analysis 211 records from six females that we could not assign unequivocally to a reproductive class. We obtained only 11 records of young males that stayed in the study area for some months after they were photographed with their mothers for the last time, but this material was insufficient to be analyzed as a separate group and was hence excluded from the analyses. All other recorded males had large bodies and large testicles and we classified them as adult males.

Photos of the same jaguar taken within 30 min by the same camera station were treated as a single record (Linkie and Ridout 2011). Two or more jaguars, even if photographed together, were treated as separate records. The timing of each record was determined by the camera log in 24-h format and transformed to its respective radian value.

We used the packages Activity v. 1.2 and Overlap v. 0.3.2 developed in R software (Ridout and Linkie 2009; Rowcliffe et al. 2014; Rowcliffe 2019) to estimate daily activity patterns, daily activity levels, and their overlaps between groups, for each jaguar sex/age/reproductive group. Daily activity patterns for each jaguar group were estimated from activity curves plotted with the Activity v. 1.2. We fitted the distribution of detection times for each jaguar group to a Von Mises kernel probability density function, using 1-h bandwidths. To compare activity patterns between jaguar sex/age/reproductive groups, we calculated the activity overlap coefficient for each pair of jaguar groups, estimated as the fraction of the interception area of the two probability density functions (Ridout and Linkie 2009). This coefficient can get values between 0 (no overlap) and 1 (complete overlap). To test if the overlap was significantly different from 0, the program compares it with a null distribution of possible overlaps created with 999 bootstrap iterations and calculates 95% confidence intervals (Ridout and Linkie 2009).

We defined daily activity level as a mean number of hours per day when a moving jaguar was recorded by the cameras. Following Rowcliffe et al. (2014), we assumed that at the hour of activity peak all animals from the same group were active. Thus, the ratio between the number of records at any hour and the records at the activity peak corresponds to the proportion of active individuals during that hour. With these assumptions, we estimated daily activity level for each age/reproductive group of jaguars by applying kernel density estimator to fit the probability density function to frequency of records during a 24-h period, using the Activity program (Rowcliffe et al. 2014; Rowcliffe 2019). It calculates the daily activity level as the value proportional to the area under the probability density function. To estimate hourly activity levels, we calculated the area under the probability curve corresponding to each hour, assuming that at the peak hour the mean activity lasted 60 min. We compared absolute daily activity levels between jaguar groups using the Wald test within the Activity v. 1.2 package in R (Rowcliffe et al. 2014; Rowcliffe 2019).

In our study area, the sunrise is between 6:10 and 6:50, and the sunset is between 18:10 and 18:50. Here, we use the following definitions: night from 20:00 to 5:00, morning from 5:00 to 8:00, day from 8:00 to 18:00, and evening from 18:00 to 20:00.

Results

We collected 3,656 jaguar records with corresponding detection time for which we could assign sex, age, and reproductive status. This number included 2,214 records of twenty-four males, 1,017 records of sixteen reproductive females, 137 of five subadult non-reproductive females, and 288 of thirty-eight cubs.

In general, jaguars showed mostly nocturnal and crepuscular activity pattern (Fig. 1). They started to become active after 18:00 and remained active until 8:00, with 47.6% of records at night (between 20:00 and 5:00) and 35.5% of
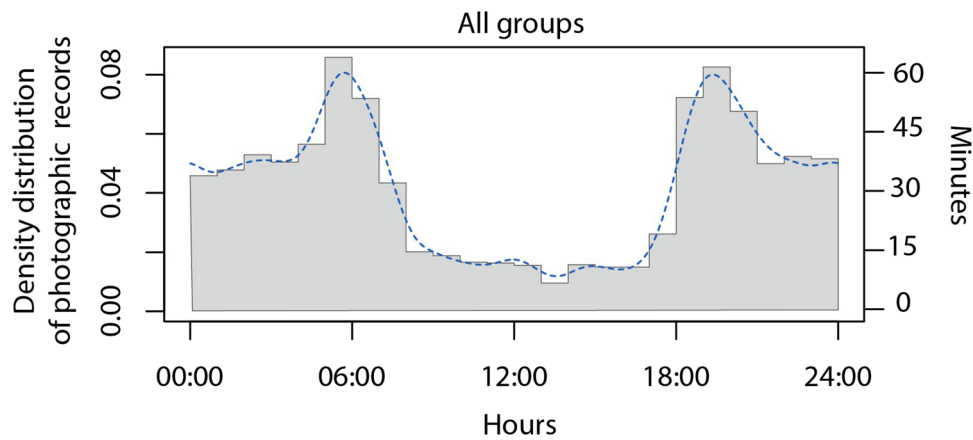
Fig. 1 Activity levels and activity patterns of jaguars (records of all jaguar groups combined) along the 24 h of the day, based on camera trapping records from Hato Piñero, Los Llanos, Venezuela. Bars (gray)—frequency of records (see SM Table S1 for numbers of records). Dashed line—activity level estimated as probability density function fit with kernel estimator to the frequency distribution of records. Left axis—estimated density function values. Right axis—mean activity level (minutes active during an hour)

records at twilight (either evening 18:00–20:00 or morning 5:00–8:00). During the nine night-hours, they were active for 5.6 h on average, while during the five twilight hours they were active for 4.1 h (Table 1). During the ten day-hours (8:00–18:00), they stayed active for only 2.0 h on average (16.9% of all records). Jaguars showed two clear activity peaks between 19:00 and 20:00 and between 5:00 and 6:00 (Table 1, Fig. 1).

Activity levels differed between sex/age/reproductive groups of jaguars (Fig. 2, Table 1). Males were active for 10.9 h per day, reproductive females for 13.2 h, non-reproductive females for 10.5 h, and juveniles for 8.7 h. Males, reproductive females, and non-reproductive females had similar activity levels during the night (5.5, 5.6, and 5.8 h, respectively) while cubs were least active (3.1 h) at that time.

During the morning and evening hours, males and reproductive females had longer activity times (4.1 and 4.2 h, respectively) than non-reproductive females (2.8 h) and cubs (3.3 h). During the day-hours, the differences were greater: males moved least (for 1.2 h) and reproductive females were active for the longest time (3.4 h on average). Non-reproductive females were active for 2.0 h and cubs for 2.3 h during the day (Table 1). The differences in activity levels between males, reproductive females, and cubs vs. non-reproductive females during the morning, males vs. reproductive females during the day, and males and reproductive females vs. cubs during the night were significant (Wald test, Table 1).
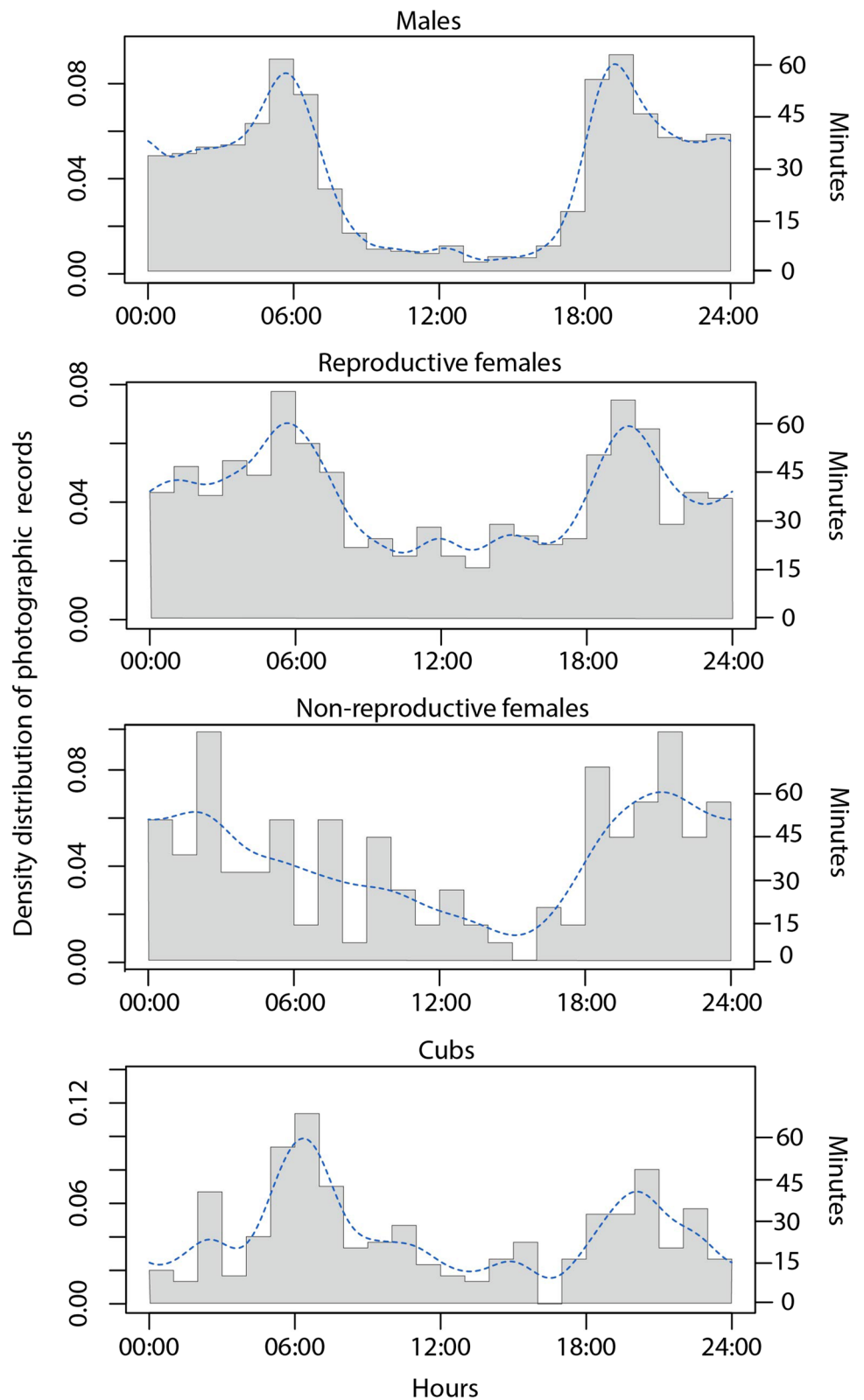
Males and reproductive females had evening and morning activity peaks at the same time: between 19:00 and 20:00 and then between 5:00 and 6:00, respectively (Fig. 3).

Table 1 Number of records (*N*) and activity levels (mean number of hours active) for the jaguar sex/age/reproductive groups, calculated for four time intervals with kernel estimator based on camera trap records from Hato Piñero, Los Llanos, Venezuela. Significant differences in the mean number of hours active per day between jag- uar groups, tested with the Wald test, are marked with the symbols: a M-NRF $p < 0.00$, b RF-NRF $p < 0.05$, c NRF-C $p < 0.00$, d M-RF $p < 0.00$, e M-C $p < 0.03$, f RF-C $p < 0.02$ (*M* males, *RF* reproductive females, *NRF* non-reproductive females, *C* cubs)

| Day period/time	Males		Reproductive females		Non-reproductive females		Cubs		All jaguars	
	N	Hours active	*N*	Hours active	*N*	Hours active	*N*	Hours active	*N*	Hours active
Morning 5:00–8:00	445	2.2a	191	2.5b	18	1.4a,b,c	80	2.4c	734	2.3
Day 8:00–18:00	254	1.2d	263	3.4d	26	2.0	75	2.3	618	2.0
Evening 18:00–20:00	384	1.9	133	1.7	18	1.4	30	0.9	565	1.8
Night 20:00–5:00	1,131	5.5e	430	5.6f	75	5.8	103	3.1e,f	1,739	5.6
Total 0:00–24:00	2,214	10.9	1,017	13.2	137	10.5	288	8.7	3,656	11.7

Fig. 2 Activity levels and activity patterns of the jaguar sex/ age/reproductive groups along the 24 h of the day in Hato Piñero, Los Llanos, Venezuela. Symbols as in Fig. 1

Non-reproductive females did not show morning or evening activity peaks but instead they were most active in the night between 21:00 and 22:00 and between 2:00 and 3:00. Cubs had activity peaks between 20:00 and 21:00 and between 6:00 and 7:00, slightly different than reproductive females (Fig. 3). The overlapping of activity patterns was highest

Fig. 3 Overlap of kernel density curves between jaguar age/sex/reproductive groups based on records from camera trapping in Hato Piñero, Los Llanos, Venezuela. We fitted a Von Mises kernel probability density function to the distribution of time of detection records of jaguars and we calculated the overlap coefficient Δ based on 999 bootstrap iterations with 95% confidence intervals (Table 2). The gray area under the density indicates extent of overlapping in activity levels during each hour
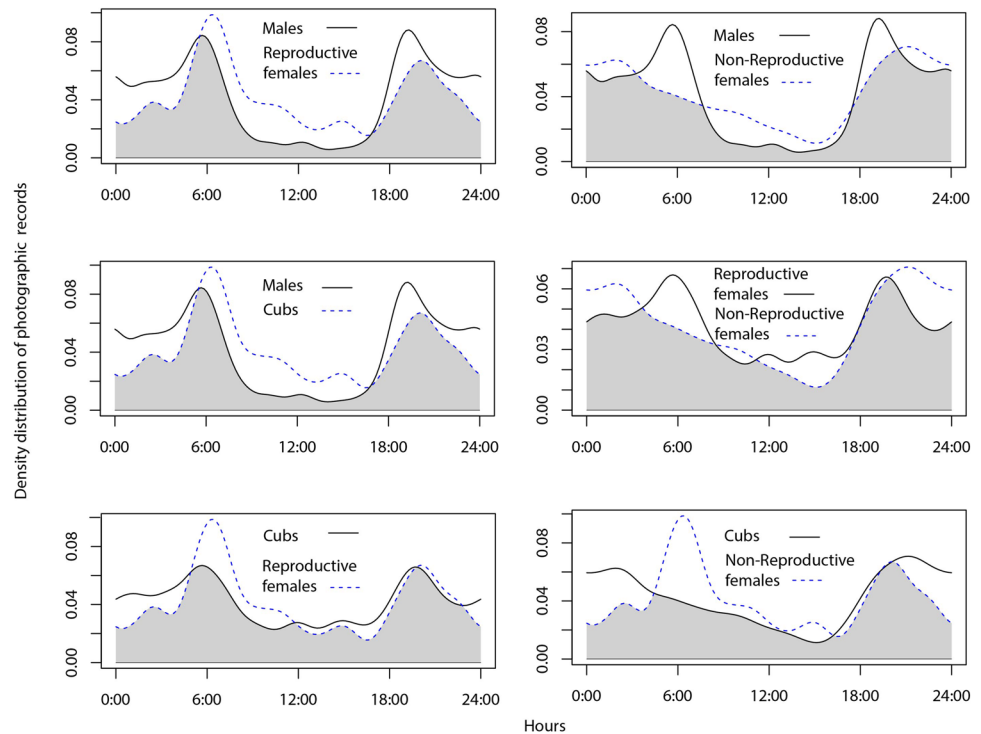
between cubs and reproductive females ($\Delta = 0.87$) and lowest between cubs and males ($\Delta = 0.79$) (Table 2).

Discussion

We estimated daily movement activity levels and movement activity patterns for the jaguar population and its sex/age/reproductive groups in Hato Piñero. Jaguars in general showed low movement activity during the daylight hours, they started to move after the sunset, and they were fairly active through the night until 2 h after the sunrise. There were two clear activity peaks: 1 h after the sunset and just before the sunrise for all jaguars pooled. This pattern coincides with other camera trapping studies (Harmsen et al. 2011; Foster et al. 2013; Herrera et al. 2018) and telemetry studies (Schaller and Crawshaw 1980; Cavalcanti and Gese 2009), where jaguars also exhibited mostly night and crepuscular activity patterns, although in some studies (e.g., Crawshaw and Quigley 1984) they had more diurnal activity. Several previous studies have already provided data evidencing that crepuscular and night activity of carnivores may result from synchronization with those of their prey (Porfirio et al. 2017; Nagy-Reis et al. 2019; Rasphone et al. 2020). Since the major prey species killed by jaguars in Hato Piñero included collared peccary (*Pecari tajacu*), capybara (*Hydrochoerus hydrochaeris*), and white-lipped peccary (*Tayassu pecari*) (Polisar et al. 2003), it has been suggested that the prevailing nocturnal activity of jaguars in this region may be associated with activity patterns of these animals (Scognamillo et al. 2003). However, more recent data showed that all these three prey species have highly diurnal activity patterns in Hato Piñero (Vivas López 2019). Therefore, in the case of the jaguar, other factors must drive their activity patterns. Rabinowitz and Nottingham (1986) found that in Belize the radio-collared jaguars changed their

Table 2 Activity patterns overlap coefficient (Δ) between jaguars of different sex/age/reproductive groups (95% CI)

	Males	Reproductive females	Non-reproductive females	Cubs
Males	1			
Reproductive females	0.84 (0.81–0.87)	1		
Non-reproductive females	0.84 (0.79–0.89)	0.86 (0.80–0.92)	1	
Cubs	0.79 (0.73–0.83)	0.87 (0.81–0.92)	0.79 (0.71–0.86)	1

behavior to more nocturnal when they entered hunting areas and to more diurnal when they were in the protected areas. In Hato Piñero, jaguars are safe from hunting although they can be hunted when going outside of this protected area.

Our estimate of the jaguar activity level (duration) is the first such an estimate for this felid. Our most important finding is showing that jaguars of different age/sex/reproductive groups had different activity levels, possibly related to their energy expenditures. According to our hypothesis, reproductive females which have to take care of the cubs, hunt for the cubs and for themselves, defend territory, and mate had the longest activity time. Males, which hunt for themselves, patrol their territories, mate, and defend their females, had the second longest activity. Non-reproductive females that just hunt for themselves had still lower activity level, whereas cubs that are not yet breeding and do not need to hunt were least active (about 5 h less than their mothers). Similar relationships between activity and reproductive status were observed in other carnivores, including felids (e.g., Schmidt 1999; Kolowski et al. 2007; Schmidt et al. 2009; Manfredi et al. 2011; Martins and Harris 2013; Quaglietta et al. 2018).

Jaguar cubs and non-reproductive (mostly subadult) females had also different activity patterns with different peak hours than adult (both males and females) jaguars. It coincides with earlier observations from the same study area in Hato Piñero that females leave cubs hidden with a prey hunted on earlier days for some hours while they go to hunt a new prey (Jędrzejewski et al. 2014). In this way, cubs are additionally protected from encounters with likely infanticidal males (Tortato et al. 2017) or other predators that may pose a danger to them. High coincidence of male and reproductive female activities with exactly the same peak hours may result from frequent interactions between them and from the fact that male activity is largely related to gaining information on the reproductive status of females, mating, and defending females from other males (de Azevedo and Murray 2007; Cavalcanti and Gese 2009; Brooke and Donahue 2020). Activity patterns of subadult pre-reproductive females did not coincide with male's activity in our study.

To estimate jaguar activity level and pattern, we used data from camera trapping which registered mostly movement activity, as most cameras were set at jaguar trails. They did not register such activities as hunting (direct attacks on prey) or feeding, although mating was recorded fairly frequently and occasionally they recorded playing. Thus, our estimate is comparable with other camera trapping estimates but would not be fully comparable with other types of studies, e.g., telemetry which can detect and classify other types of behavior as activity as well. Additionally, our estimate of activity level was based on the assumption that at the peak of activity all jaguars from the same age/sex/reproductive status group were active (Rowcliffe et al. 2014). This assumption seems plausible,

especially for males, reproductive females, and cubs, as their activity peaks were obviously related to sunset and sunrise that likely synchronized movements of different individuals. The activity pattern of non-reproductive females was more dispersed and possibly less synchronized. If not all individuals of this group were active during the peak hour, our estimate of the duration of activity might be somewhat overestimated for non-reproductive females. Additionally, number of records was fairly small for this group, making this estimate less certain. We could not estimate activity level and pattern for analogous sub-adult males group because their records were restricted only to a few cases of juveniles staying shortly in the study area after they had left their mothers. It is likely that young dispersing males avoid areas with established adult males until they grow big enough to combat for a territory (Eisenberg 1986; Macdonald et al. 2010).

Although our activity analyses were based on a very large data set, which allowed us to analyze activity levels with relatively high precision of 1-h intervals, it is likely that still larger data would allow for a more detailed analysis and for relating better the activity levels to different life or reproductive stages. For example, we pooled together all the data from reproductive females, while their behavior may differ between periods of mating, pregnancy or periods of cub rearing. Effect of different phases in the reproductive cycle on activity budgets and other behaviors were shown by telemetry studies in the Eurasian lynx and Amur tigers (Schmidt 1999; Jędrzejewski et al. 2002; Petrunenko et al. 2020). Long-term projects that have a chance to collect larger data sets are important to increase precision of activity estimates and understanding the factors that determine them.

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