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TEMPORAL ACTIVITY PATTERNS OF TERRESTRIAL MAMMALS IN LOWLAND RAINFOREST OF EASTERN ECUADOR

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Abstract. Daily activity patterns of most Neotropical mammals are not well described although general patterns (nocturnal, diurnal) are known. Yet general categories often do not reflect variation in activity over time or among different habitats or regions. We used camera traps to learn more about how daily activity patterns of mammals vary at a site in lowland rainforest of Ecuador. Cameras were deployed along trails at Tiputini Biodiversity Station during two periods: January 2005 to August 2008 and February 2010 to January 2012. We obtained 3649 photographs of 32 species. There was a pronounced peak of overall activity in early morning (06:00 – 08:00 h), reflecting the combined activity of several species, including *Mazama americana* red brocket deer, *Myoprocta pratti* green acouchy, *Pecari tajacu* collared peccary, and *Sciurus igniventris* northern Amazon red squirrel, among others. Daily activity of some species (e.g. *Tapirus terrestris* South American tapir) differed between the two sample periods, whereas that of others (e.g. *M. americana*) did not. Variation in activity across months also was pronounced in some species (e.g. *M. americana*, *T. terrestris*, *Dasyprocta fuliginosa* black agouti, *Tayassu pecari* white-lipped peccary), perhaps in relation to changes in rainfall patterns or habitat use. In addition, comparisons with previously published data demonstrated that daily activity patterns may vary locally between habitats and over broader geographic scales.

Keywords: activity, Amazonia, camera trap, daily activity, Ecuador, mammal.

INTRODUCTION

Daily activity patterns of many tropical animals are known in general terms (i.e. whether a species is mostly nocturnal or diurnal) (e.g. Emmons & Feer 1997) but details of these patterns are less well described. Information on activity patterns is, however, needed both for increasing our basic understanding of the ecology of many tropical organisms and, potentially, for understanding impacts of human activity on the behavior of affected species (e.g. those that are hunted). Patterns of activity can reveal aspects of ecology and behavior not shown by more general categories. For example, related or ecologically similar species, such as *Mazama americana* (red brocket deer) and *M. gouazoubira* (grey brocket deer), may be active at different times of the day, perhaps to reduce potential for competition (Tobler *et al.* 2009). In other cases, predator activity may vary geographically to match the activity of potential prey, as shown for *Panthera onca* (jaguar; Maffei *et al.* 2004, Weckel *et al.* 2006). In other cases, patterns of activity may vary with habitat; activity of *Tapirus pinchaque* (mountain tapir), for example, declined along trails within montane forest while it increased at mineral licks in the same area (e.g. Lizcano & Cavelier 2000). Some animals, such as *M. americana*, may alter daily activity patterns to reduce possibilities of encountering hunters (Di Bitetti *et al.* 2008; see also Bridges *et al.* 2004). Although relatively detailed accounts of diurnal activity patterns of Neotropical mammals exist for some species (e.g. *Priodontes maximus* giant armadillo, Noss *et al.* 2004; *Procyon cancrivorus* crab-eating racoon, Arispe *et al.* 2008; *Oncifelis geoffroyi* Geoffroy's cat Cuéllar *et al.* 2006; *Leopardus pardalis* ocelot, Emmons 1988, Di Bitetti *et al.* 2006; *Panthera onca*, Maffei *et al.* 2004; *Tapirus pinchaque*, Lizcano & Cavelier 2000; *Tapirus terrestris* South American tapir Noss *et al.* 2003; *Mazama americana* and *M. nana* dwarf brocket deer, Di Bitetti *et al.* 2008), there are few that provide details on multiple species from the same location (Gómez *et al.* 2005, Weckel *et al.* 2006, Kasper *et al.* 2007, Tobler *et al.* 2009). Such studies are needed, however, to better

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understand how community composition might influence activity patterns of the component species. Fortunately, increasing availability of camera traps has provided more opportunities for determining activity patterns of multiple species simultaneously and how those activity patterns vary over space and time (Bridges & Noss 2011).

In previous studies (Blake *et al.* 2010, 2011) we documented activity (as measured by numbers of photographs) of mammals and birds at four mineral licks (sites that mammals and birds visit to eat soil or drink water) located within Tiputini Biodiversity Station, Ecuador, the site of the current study. Over an approximately four-year period we obtained 7889 photographs representing 23 mammal species and 888 photographs representing 15 bird species. Tapirs (*Tapirus terrestris*), peccaries (*Pecari tajacu*, *Tayassu pecari*), deer (*Mazama americana*), and pacas (*Cuniculus paca*) were the most frequent mammal visitors, guans (*Pipile pipile*) and pigeons (*Columba plumbea*) the commonest birds. Use of licks varied diurnally and seasonally but patterns of use varied among species and sites.

Given that activity patterns of mammals may vary among habitats (Tobler *et al.* 2009), the major goal of this study was to document daily activity patterns of non-volant mammals within *terra firme* forest (i.e. not at mineral licks) of lowland Ecuador. We examine hourly and monthly variation in activity as measured by numbers of photographic records obtained from cameras placed along trails located within Tiputini Biodiversity Station. The station is not affected by hunting so results provide a good baseline for comparison with other areas that are affected by human activities. Further, because there are few data on activity patterns in lowland rainforest, the data allow comparisons with previous studies conducted in different regions of the Neotropics.

METHODS

Study site. We conducted our research at Tiputini Biodiversity Station (TBS), Orellana Province, Ecuador (~0°37'S, 76°10'W, 190-270 m a.s.l.), a 650-ha reserve located on a tract of undisturbed lowland rainforest within the ~2.7-million-ha Yasuní Biosphere Reserve, one of the most biologically diverse regions of the world (Bass *et al.* 2010). Approximately 30 km of trails provide access to most areas of the station. The station and nearby areas are dominated by *terra firme* forest; várzea forest, palm swamps, and various successional habitats also are present. Mean annual precipitation at Yasuní Research Station, approximately 30 km WSW of TBS, is about 3100 mm. Rainiest months are from April through June; January and August are relatively dry, with January often very dry (personal observations) (Fig. 1).

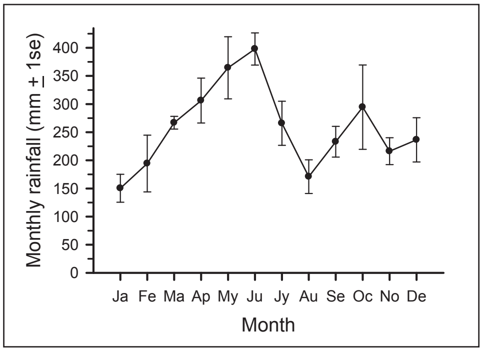

FIG. 1. Monthly rainfall (mm ± 1 s.e.) based on data from Yasuní Research Station, 2000–2010; months with more than one or two days with missing data were omitted from calculation of monthly values. Most monthly values are based on 6 years of data, with some based on 4, 5, or 7 years.

Camera trapping. Cameras triggered by an infrared heat-and-motion detector were deployed during two sample periods: mid-January 2005–August 2008 and February 2010– January 2012. We used film-based camera traps (Highlander Photoscout, PTC Technologies) during the first sampling period and digital camera traps (Cuddeback Capture) during the second. Pairs of cameras were located approximately 1-1.2 km apart along preexisting trails within *terra firme* forest. Cameras were placed at sites that showed evidence of animal activity (e.g. tracks) or at sites where occurrence was likely (based on topography and local knowledge). Cameras were not placed where natural resources (e.g. patches of fruit) might be likely to attract animals; we also did not use any chemical attractants. Two cameras were placed at each site (8 sites during the first period, 10 sites during the second), on opposite sides of the trail, approximately 0.75-1 m off the ground. We set cameras with a minimum time between photographs of 5 min. Cameras remained continuously activated (except when malfunctions occurred); date and time were automatically stamped on each photograph. Cameras were checked at approximately monthly intervals to replace film, change SD cards, and check batteries. All images were labeled with location, camera, date, time, and species.

Analyses. We summarized images by species, hour, and date. We classified photographs as belonging to independent records if more than 30 min had elapsed between consecutive photographs of the same species at a given location (see Blake *et al.* 2011). Activity was evaluated in terms of number of photographs, percentage of photographs, or photographs/100 trap-days, depending on the analysis. We encountered many more problems with the film-based cameras and, as a consequence, we only used data from the second period when calculating number of photographs per 100 trap-days. Problems with the digital camera traps increased towards the end of the study. We calculated number of trap-days from the time the camera was placed in operation until the last photograph was taken (based on the date and time stamp on the photographs). We classified records by hour, starting at midnight, to examine diurnal patterns of activity, and by month to examine overall activity irrespective of hour.

When appropriate, we compared observed numbers of records to expected numbers using chi-square tests (Whitlock & Schluter 2009). We based expected values on an even distribution during 24 hours to compare activity by hour. To compare use across months, we calculated expected numbers based on number of trap-days cameras were operational during each month (summed across years) so expected values for visits/month were standardized by sample effort. We compared activity between species with contingency table tests (i.e. comparing number of photos by hour). We used correlation analyses to examine the relationship between average monthly activity and average monthly rainfall recorded at Yasuní Research Station (Fig. 1). Data were checked for assumptions of normality (Shapiro-Wilk test) and homogeneity of variances (Levene's test) before parametric tests were applied.

RESULTS

Hourly activity patterns. A total of 32 species of mammals was photographed, including 29 during the first period (1796 independent records over 7222 trap-nights) and 30 during the second period (1853 records over 6178 trap nights) (Table 1). Three of those species are listed as Vulnerable (IUCN 2012): *Myrmecophaga tridactyla, Pridontes maximus*, and *Tapirus terrestris*; five are listed as Near Threatened: *Atelocynus microtis, Speothos venaticus, Panthera onca, Leopardus wiedii*, and *Tayassu pecari*. Nineteen species were photographed at least 10 times in one of the two samples (Table 1); 11 species were represented by at least 100 total photographs, accounting for about 88% of the overall total. There was a pronounced peak of combined activity from about 06:00 to 08:00 h during both sample periods (Fig. 2), reflecting the activity patterns of several species (e.g. *Mazama americana, Myoprocta pratti, Peccari tajacu, Sciurus igniventris*; common names in Table 1).

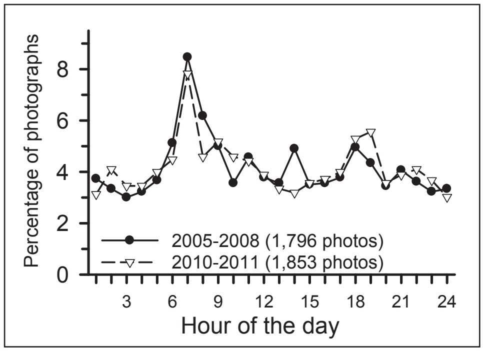

FIG. 2. Hourly variation in number of photographs (percentage of total) of all mammals combined recorded in camera traps at Tiputini Biodiversity Station, Ecuador, 2005-2008 and 2010-2011.

Most major groups of mammals were represented both by diurnal and nocturnal species. Among Cingulata, for example, armadillos were primarily nocturnal, with both species showing more activity after than before midnight (Fig. 3). In contrast, *Myrmecophaga tridactyla* was primarily diurnal with a peak of activity during the late afternoon.

Three of the five rodent species were primarily diurnal and two were nocturnal (Fig. 3). *Sciurus igniventris* showed an abrupt increase in activity at daylight, with a declining number of photographs throughout the day (perhaps reflecting a shift to more arboreal activity). *Myoprocta pratti*, one of the commonest species in photographs (Table 1), had a strong bimodal pattern, with a much stronger peak around 07:00 h and a somewhat less pronounced peak from about 18:00 to19:00 h. *Dasyprocta fuliginosa* was active throughout the day, with no pronounced peak. Both the paca and spiny rats were nocturnal but differed in their hours of activity (Fig. 3) (χ^2 = 30.1, df = 7, P < 0.001). *Cuniculus paca* was more active in the middle of the night, whereas

TABLE 1. Numbers of photographs of mammals recorded along trails during two sample periods (2005-2008, 2010-2011) and percentage of photographs that were nocturnal (N%; 18:30-05:30 h), diurnal (D%; 06:30-17:30 h), or crepuscular (C%; 05:30-06:30 h and 17:30-18:30 h) based on data from both samples combined. Nomenclature follows Wilson & Reeder (2005).

Family	*Scientific name*	Common name	No. photos 05-08	No. photos 10-11	N%	D%	C%
Myrmecophagidae	*Myrmecophaga tridactyla*	giant anteater	13	10	13	70	17
Dasypodidae	*Priodontes maximus*	giant armadillo	29	26	85	4	11
Dasypodidae	*Dasypus novemcinctus*	nine-banded armadillo	114	86	97	2	1
Canidae	*Atelocynus microtis*	short-eared dog	31	12	12	76	12
Mustelidae	*Eira barbara*	tayra	15	25	3	94	3
Felidae	*Leopardus pardalis*	ocelot	187	156	88	8	4
Felidae	*Leopardus wiedii*	margay	5	6	91		9
Felidae	*Puma concolor*	puma	55	37	75	20	5
Felidae	*Panthera onca*	jaguar	82	53	33	58	9
Tapiridae	*Tapirus terrestris*	South American tapir	190	267	80	13	7
Tayassuidae	*Pecari tajacu*	collared peccary	222	178	2	89	9
Tayassuidae	*Tayassu pecari*	white-lipped peccary	164	175	5	88	7
Cervidae	*Mazama americana*	red brocket deer	151	108	38	49	13
Cervidae	*Mazama gouazoubira*	grey brocket deer	22	18	0	88	12
Sciuridae	*Sciurus igniventris*	n. Amazon red squirrel	85	47	0	95	5
Cuniculidae	*Cuniculus paca*	paca	43	115	99	1	0
Dasyproctidae	*Dasyprocta fuliginosa*	black agouti	103	217	3	91	6
Dasyproctidae	*Myoprocta pratti*	green acouchy	205	257	1	46	53
Echimyidae	*Proechimys* sp.	spiny rat	37	20	96	2	2
Leporidae	*Sylvilagus brasiliensis*	Brazilian rabbit	21	6	81	0	19

Species with < 10 photos (number of photos is given for first and second sample periods): *Caluromys lanatus* (2,0), *Cebus albifrons* (4,3), *Coendou prehensilis* (0,1), *Didelphis marsupialis* (4,3), *Metachirus nudicaudatus* (0,1), *Microsciurus flaviventer* (1,0), *Procyon cancrivorus* (0,7), *Puma yagouaroundi* (2,4), *Nasua nasua* (4,5), *Saimiri sciureus* (1,4), *Speothos venaticus* (1,1), *Tamandua tetradactyla* (3,4).

Proechimys showed a peak of activity before dawn and a second peak in the early part of the night. *Sylvilagus brasiliensis*, the only rabbit, was irregularly active during the night but was not photographed during daylight.

Five species of ungulates were recorded along trails. *Tapirus terrestris*, although active during the night and day, had a strong bimodal pattern of activity, with one peak of activity from about 03:00 to 06:00 h and a second, more sustained period of activity from about 20:00 to 22:00 h; there were relatively few records from late morning until evening (Fig. 4). The pattern differed somewhat between samples ($\chi^2 = 22.1$, df = 12, $P = 0.036$), with a more pronounced 06:00 h peak in the first sample and around 22:00 h in the second. Both species of peccaries were largely diurnal (Table 1, Fig. 4), with few records before 06:00 h or after 18:00 h. *Pecari ta-*

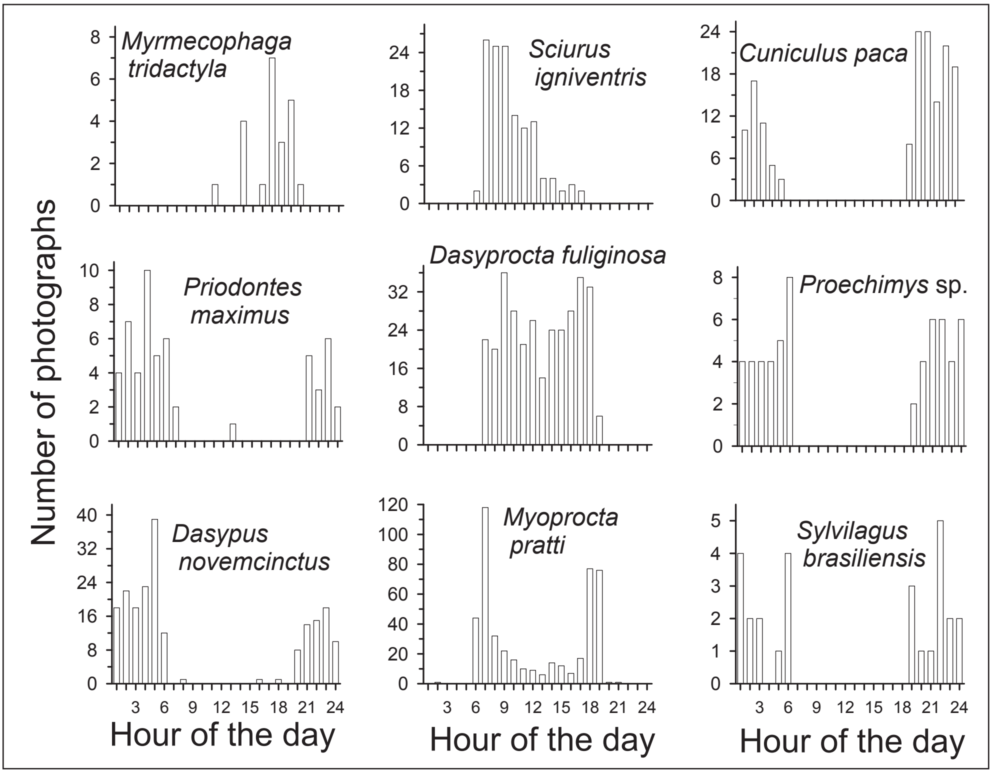

FIG. 3. Hourly variation in number of photographs of edentates, rodents, and lagomorphs recorded in camera traps at Tiputini Biodiversity Station, Ecuador. Data from both samples combined.

jacu, the smaller of the two species, had a particularly pronounced peak of activity in the earlier part of the day during the first sample, with activity declining into the afternoon; during the second period, this early morning peak was not evident and the greatest activity was late morning to early afternoon. *Tayassu pecari*, in contrast, was more consistently active throughout the day. Differences between the two species were not, however, pronounced (χ^2 = 17.5, df = 12, P = 0.13). Two species of *Mazama* showed distinctly different activity patterns. The less common *M. gouazoubira* was not active at night and was somewhat more active during the middle part of the day and again near dusk (Table 1, Fig. 4). *Mazama americana*, in contrast, was active throughout the day and night, with a strong peak in the early morning and a less pronounced peak in the late afternoon and early evening (Fig. 4). The pattern of activity did not differ between samples (χ^2 = 3.8, df = 11, P = 0.97).

Five carnivores were sufficiently common to evaluate their hourly activity. *Leopardus pardalis* was the most photographed and the most nocturnal, although there were photographs from most hours of the day (Fig. 4). There was a pronounced peak in activity around 22:00 h in both samples. *Panthera onca*, the largest carnivore, was active throughout the day and night but was more active during daylight, with peaks in the early morning and late afternoon; jaguars were least active from about 02:00 to 05:00 h (Table 1, Fig. 4). In contrast, *Puma concolor*, although active during the day as well, was more active at night with a peak in activity around midnight and a lesser peak around 05:00 h. Differences in activity among the three felids were significant when all three were considered together (χ^2 = 184.6, df = 18, P < 0.001) and when pairs were considered separately (*Leopardus* vs. *Panthera*: χ^2 = 177.0, df = 9, P < 0.001; *Leopardus* vs. *Puma*: χ^2 = 28.7, df = 9, P < 0.001; *Panthera* vs. *Puma*: χ^2 = 42.5, df = 9, P < 0.001). Both *Atelocynus*

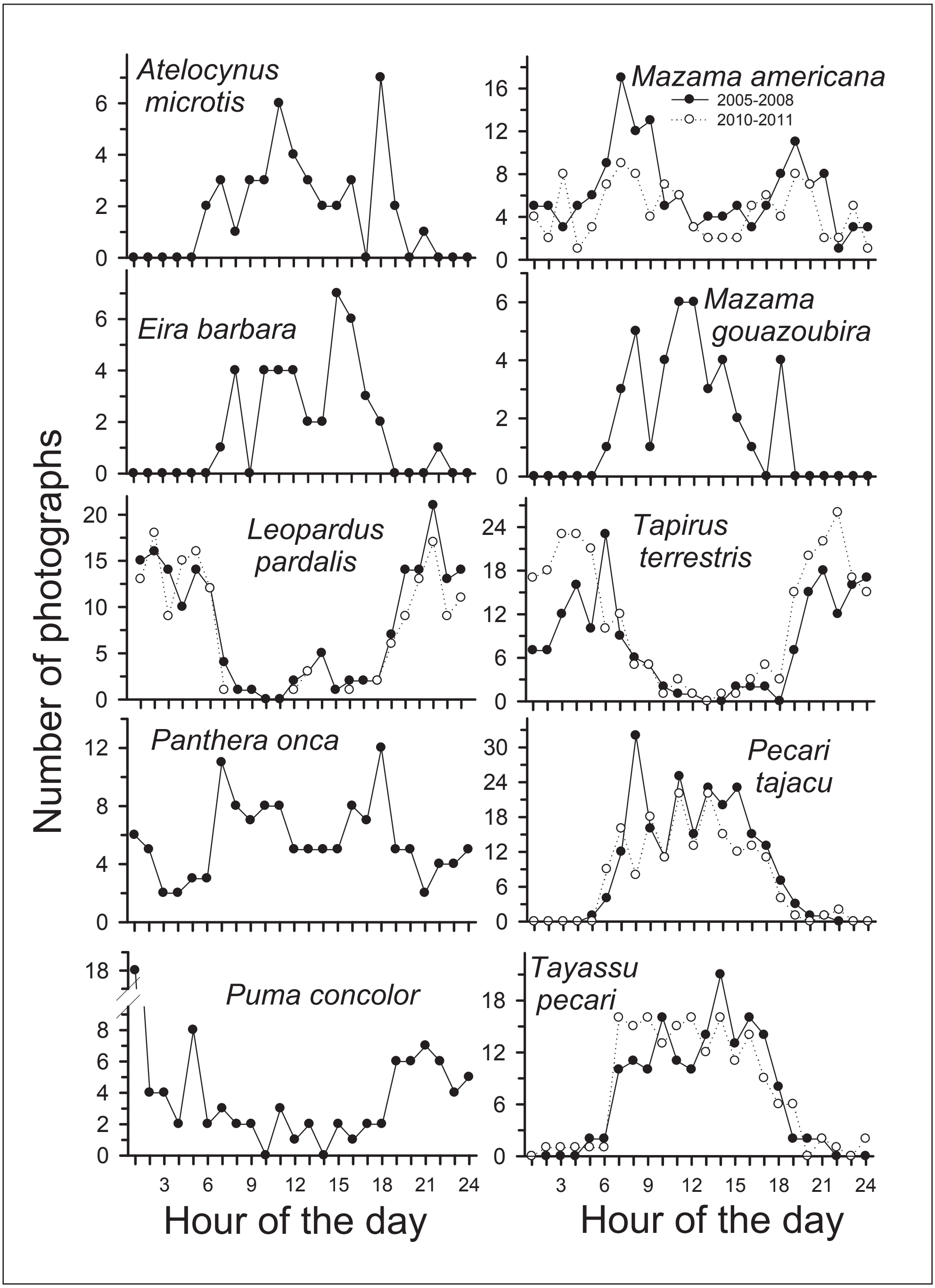

FIG. 4. Hourly variation in number of photographs of ungulates and carnivores recorded in camera traps at Tiputini Biodiversity Station, Ecuador. Results from both sample periods (2005-2008, 2010-2011) are shown for species with sufficient number of records; data are combined for less common species.

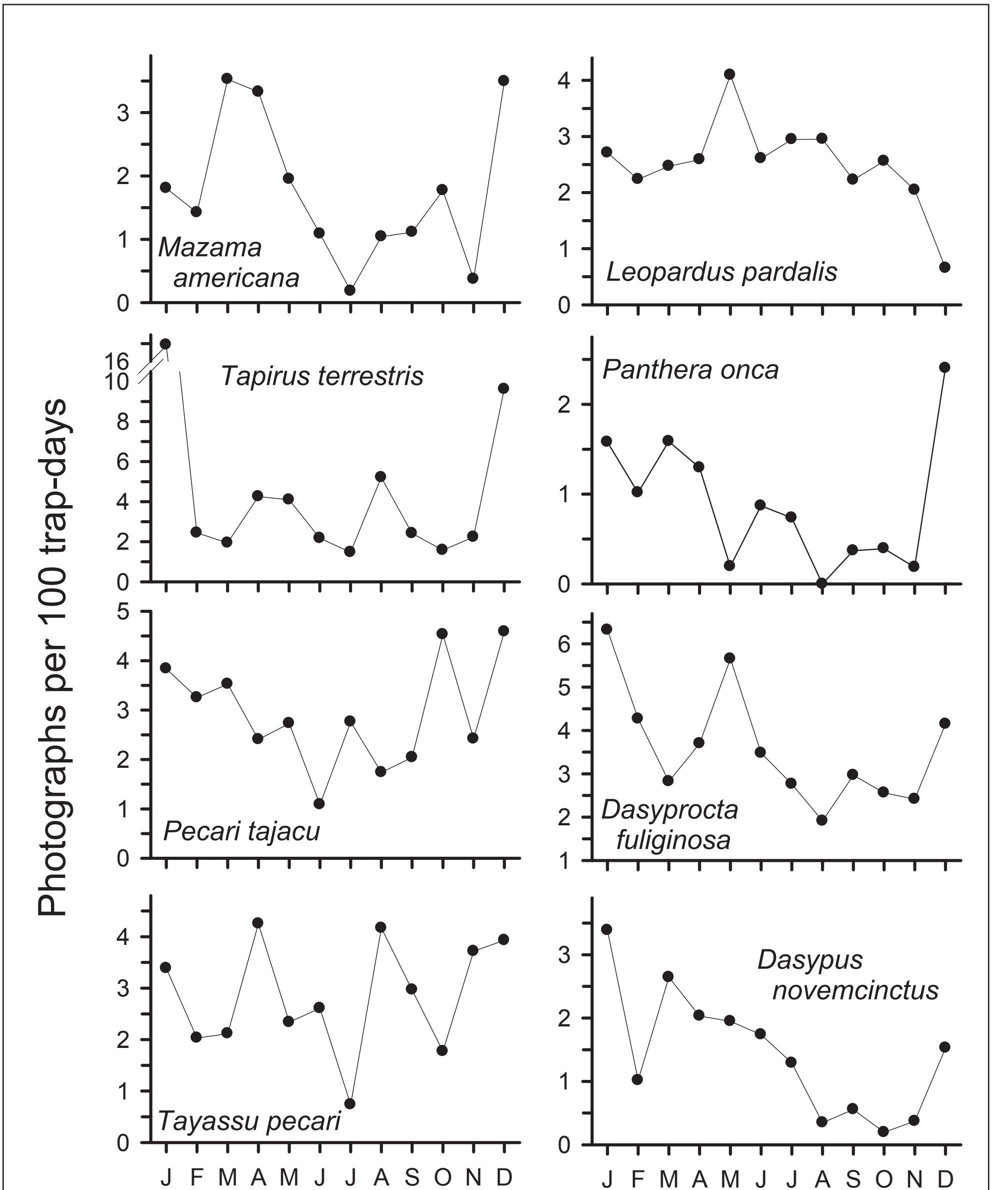

FIG. 5. Monthly activity (as measured by number of photographs/100 trap-days) of common mammals recorded in camera traps at Tiputini Biodiversity Station, Ecuador, 2010-2011.

and *Eira* were primarily diurnal, with the former species showing a peak in activity in late morning and late afternoon, while the latter showed a peak in the early afternoon (Fig. 4).

Monthly activity patterns. Most species were not represented by a sufficient number of photographs to justify analyzing activity by month. Of those species examined (Fig. 5), most showed considerable variation in activity between months. Ungulates, particularly *Mazama americana*, tended to show a decrease in activity during the middle of the year, a period of greater average rainfall, and greater activity during the drier months (generally December-March). Activity was not, however, correlated with long-term average monthly rainfall ($r < 0.0$, $P > 0.10$, all comparisons). *Leopardus pardalis* activity remained relatively constant throughout much of the year but declined in December, a month with a sharp increase in *Panthera onca* activity. *Dasyprocta fuliginosa* and *Dasypus novemcinctus* exhibited relatively similar patterns, with activity generally decreasing from early to later in the year before increasing again in December.

DISCUSSION

Results from the current study are largely concordant with basic accounts of natural history (i.e. whether a species is most active during the day or night; Emmons & Feer 1997) as well as previous studies on hourly activity patterns (e.g. Kasper *et al.* 2007, Tobler *et al.* 2009). In the following, we compare our results with those of previous studies that have used camera traps to evaluate activity patterns of Neotropical mammals.

Local variation in hourly activity. At a local scale (i.e. within TBS), activity patterns often differed between mineral licks (Blake *et al.* 2011) and *terra firme* forest trails located in the same 650-ha reserve. Given that all licks were within approximately 500 m of trails where cameras were located, licks and trails would have been equally accessible to mammals. Thus differences likely reflect behavioral differences in patterns of habitat use. For example, two primates, *Alouatta seniculus* (Venezuelan red howler monkey) and *Ateles belzebuth* (white-bellied spider monkey) were common at mineral licks (Blake *et al.* 2010, Link *et al.* 2011) but neither species was photographed along trails. Felids, by contrast, showed an opposite pattern, with no records of *Panthera onca*, one of *Puma concolor*, and only five of *Leopardus pardalis* from mineral licks but many more records along trails.

Species that were frequently photographed at both licks and along trails often showed distinctly different patterns of hourly activity. *Tapirus terrestris* occurrence at mineral licks was, for example, most pronounced around 21:00 h, and did not show the same peak around 06:00 h as in the present study. Similarly, hourly activity of *Tapirus pinchaque* (mountain tapir) differed between mineral licks and trails (Lizcano & Cavelier 2000), suggesting that animals used the habitats on different time schedules. In contrast to tapirs, activity of peccaries was similar along trails and at mineral licks (Blake *et al.* 2011), and similar to the pattern observed in Peru (Tobler *et al.* 2009). *Mazama americana*, one of the most frequently photographed species at mineral licks (Blake *et al.* 2011), had an early morning peak in activity at mineral licks that was approximately two hours earlier than along trails. Although it was active throughout the day at mineral licks, as along trails, there was no secondary peak of activity in the early evening.

Geographic variation in hourly activity. Many of the species recorded by cameras at TBS have also been sampled with cameras in other regions, allowing a comparison of activity patterns across a larger spatial scale. In dry forest of Bolivia, *Tapirus terrestris* exhibited a peak in activity around midnight (Noss *et al.* 2003) so did not show a bimodal activity pattern as seen in this study and that of Lizcano & Cavelier (2000). Amount of activity during the day also varied geographically, with tapirs in Belize more nocturnal (97% of photographs; Weckel *et al.* 2006) than in Ecuador or Bolivia. Paralleling tapirs, both peccaries also were more nocturnal in Belize (Weckel *et al.* 2006) than in the present study but were still primarily diurnal. *Mazama americana* showed both an early morning and early evening peak in activity in Peru (Tobler *et al.* 2009), as in the present study. Similarly, a bimodal pattern of activity also was noted in Argentina (Di Bitetti *et al.* 2008), although the first peak was earlier in the morning. *Mazama americana* also was more diurnal in its activity in Belize (69% of photographs) than in other regions. Although not as common at TBS, *M. gouazoubira* was almost entirely diurnal, as was the case in Peru (Tobler *et al.* 2009). Temporal resource partitioning may be a partial explanation for such offsetting patterns of species that have similar diets, such as the two species of *Mazama* (Tobler *et al.* 2009). A similar explanation may hold for *Cuniculus paca* and *Dasyprocta* spp. (Gomez *et al.* 2006, Blake *et al.* 2011).

Jaguars also demonstrate geographic differences in activity. Although active both day and night in most areas, jaguars were largely nocturnal in Belize, in contrast to the current study (57% diurnal). In Bolivian dry forests, jaguars were recorded infrequently from 09:00 to 15:00 h, with peaks from around 03:00 to 06:00 h and from 18:00 to 22:00 h

(Maffei *et al.* 2004). Such differences in activity may reflect differences in the diurnal activity patterns of their preferred prey, *Dasypus* and *Cuniculus* in Belize (Weckel *et al.* 2006), *Mazama* and *Pecari tajacu* in Bolivia (Maffei *et al.* 2004). Although there are no data on the preferred prey of jaguars at our site, peccaries were a preferred prey in lowland forest in Peru (Emmons 1987). If also true at our site, peccary activity may account for the greater daytime activity of jaguars in the current study.

Ocelot activity also varied somewhat between locations. Di Bitetti *et al.* (2006), for example, found peaks in activity around 22:00 h, similar to the current study, and from 06:00 to 07:00 h, with a decline in the middle of the night. Emmons (1988) also found a bimodal pattern of greater activity before midnight and then again a few hours later. Kasper *et al.* (2007) found a peak in activity from about 20:00 to 22:00 h. In all studies, ocelots were more active at night but still showed some level of activity during daylight hours. Many of the preferred prey of ocelots (e.g., *Proechimys*, *Myoprocta*, and other small rodents; Emmons 1987) also are nocturnal.

Monthly variation in activity. Variation in monthly activity levels was pronounced for most species that could be examined, but showed little agreement between species. Reduced activity during some of the wetter months might reflect changes in behavior (less movement), changes in habitats used (less activity along trails), or perhaps movement away from the area sampled by cameras. *Tayassu pecari*, for example, is known to move over extensive distances and numbers clearly fluctuate at the station (pers. obs.). The decline in activity from January to June along trails also occurred at mineral licks (Blake *et al.* 2010), suggesting that the decline in activity may have reflected changes in numbers at the station. Yet the smaller *Pecari tajacu* exhibited a similar level of variation and is not known to move over large distances. Its activity along trails (declining from early to mid-year and then increasing again) was not matched by activity at mineral licks, where activity fluctuated throughout the year without a distinct pattern. Interactions between species might also influence activity. The decline in activity of ocelots in December coincided with a sharp increase in activity of the much larger and dominant jaguar. That increase in *Panthera* activity also coincided with increased activity of potential prey (e.g. *Mazama americana*). With our current data, we are not able to distinguish between these possibilities.

Most studies that have used camera traps to evaluate activity patterns or abundance have been relatively short and have not considered variation throughout the year. Given that most species show considerable variation between months in numbers of photographs, it is evident that longer-term studies are needed to fully evaluate patterns of activity of Neotropical mammals. Daily activity patterns also vary over time and space, suggesting that multiple factors likely interact to determine patterns of activity.

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