



## Activity patterns of tayra (*Eira barbara*) across their distribution

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Species' activity patterns are driven by the need to meet basic requirements of food, social interactions, movement, and rest, but often are influenced by a variety of biotic and abiotic factors. We used camera-trap data to describe and compare the activity patterns of the relatively poorly studied tayra (*Eira barbara*) across 10 populations distributed from the south of Mexico to the north of Argentina, and attempted to identify biotic or abiotic factors that may be associated with variation in level of diurnality. In a subset of sites we also aimed to document potential seasonal variation in activity. We used a kernel density estimator based on the time of independent photographic events to calculate the proportion of diurnal, crepuscular, and nocturnal activity of each population. Tayras were mostly active during diurnal periods (79.31%, 759 records), with a lower proportion of crepuscular activity (18.07%, 173 records) yet we documented some variation in patterns across the 10 study areas (activity overlap coefficient varied from  $\Delta_4 = 0.64$  to  $\Delta_1 = 0.95$ ). In northern localities, activity peaked twice during the day (bimodal) with most activity occurring in the morning, whereas closer to the geographical equator, activity was constant (unimodal) throughout the day, peaking at midday: activity either was unimodal or bimodal in southern

localities. Despite investigating multiple potential abiotic and biotic predictors, only latitude was associated with variation in the proportion of diurnal activity by tayras across its range, with increased diurnal activity closer to the equator. Seasonal comparisons in activity showed a tendency to reduce diurnality in dry versus rainy seasons, but the pattern was not consistently significant. This is the most comprehensive description of tayra activity patterns to date, and lends novel insight into the potential flexibility of the species to adapt to local conditions.

Key words: camera trap, carnivores, Mustelidae, Neotropics, noninvasive survey, overlap analyses

Los patrones de actividad de las especies están asociados a su necesidad de satisfacer sus requerimientos básicos de alimento, interacciones sociales, movimiento y descanso, aunque frecuentemente están influenciados por una gama de factores bióticos y abióticos. Se utilizaron datos de cámaras trampa para describir y comparar los patrones de actividad de la relativamente poco estudiada especie tayra (*Eira barbara*) a través de 10 poblaciones distribuidas desde el sur de México hasta el norte de Argentina, en un intento de identificar los factores bióticos y abióticos que pueden estar asociados a la variación en el nivel de actividad diurna. En un subconjunto de sitios se buscó documentar la potencial variación de actividad entre la temporada de lluvias y el estiaje. Se utilizó el estimador de densidad de kernel para calcular la proporción de actividad diurna, crepuscular y nocturna de cada población. Las tayras fueron principalmente activas durante periodos diurnos (79.31%, 759 registros) y en menor proporción durante periodos crepusculares (18.07%, 173 registros). En localidades del hemisferio norte, hubo dos picos de actividad durante el día (bimodal), siendo mayor durante la mañana. Por otro lado, mientras la actividad fue constante (unimodal) durante el día, hubo incrementos al mediodía para localidades cerca del Ecuador geográfico. Sin embargo, esta actividad fue unimodal o bimodal en sitios del hemisferio sur. A pesar de investigar la influencia de múltiples predictores abióticos y bióticos, solamente la latitud estuvo asociada con la variación en la proporción de actividad diurna de tayras a través de su distribución, observándose un incremento de actividad diurna en localidades cercanas al Ecuador geográfico. El coeficiente de sobreposición de los patrones de actividad de tayra osciló entre  $\Delta_4 = 0.64$  y  $\Delta_1 = 0.95$ , indicando cierta plasticidad de la especie dentro del período diurno. Esto probablemente se asocia con adaptaciones a las condiciones ambientales locales, documentándose algunas variaciones de actividad entre temporadas climatológicas en un mismo sitio. Este trabajo constituye la descripción más exhaustiva de los patrones de actividad de tayra hasta la fecha, y brinda una novedosa perspectiva de la flexibilidad potencial de la especie para adaptarse a las condiciones locales.

Palabras clave: cámaras trampa, carnívoros, Mustelidae, Neotropical, catastro no-invasivo, análisis de sobreposición.

The activity patterns of terrestrial mustelids, as with those of most vertebrates, are the result both of endogenous biological rhythms, and of behavioral adaptation to a changing environment (Aschoff 1966; Daan 1981; Rusak and Boulos 1981). Broad patterns of activity across mustelids vary from diurnal, to crepuscular, to nocturnal (Larivière and Jennings 2009); yet even within species there can be significant variation in patterns of activity, demonstrating significant plasticity in this behavioral trait. For example, American mink (*Neovison vison*) display nocturnal (Gerell 1969; Yamaguchi et al. 2003), diurnal (García et al. 2009), or cathemeral (Niemimaa 1995; Zuberogitia et al. 2006) behavior, and pine marten (*Martes martes*) can shift seasonally from a diurnal to nocturnal activity pattern (Zielinski et al. 1983). Across the family, activity patterns typically mirror the activity of their primary prey (Gerell 1969; Zielinski et al. 1983).

But a suite of additional biotic and abiotic factors combine to influence various metrics of activity in these species. Level of nocturnal activity can be influenced by nighttime luminosity (*Martes flavigula*—Grassman et al. 2005), and locomotor activity can be influenced by rainfall (*N. vison*—Melero et al. 2011). Temperature clearly exerts a strong influence, at both daily and seasonal scales, on numerous aspects of activity in temperate regions, with lower daily temperatures reducing overall movement rates (*Mustela nigripes*—Richardson et al.

1987), bouts of activity (*Pekania pennanti*—McCann et al. 2019; *Mustela nivalis*—Jędrzejewski et al. 2000), and overall activity (*P. pennanti*—Arthur and Krohn 1991; *M. martes*—Zalewski 2000). Photoperiod also appears important in temperate regions, with overall levels of activity for mink increasing (Gerell 1969) or decreasing (Niemimaa 1995) as night length increased and diurnal activity of stone martens (*Martes foina*) increasing as nights became shorter (Posillico et al. 1995). The influence of temperature and photoperiod commonly are documented at a seasonal scale, and it may be hard to identify true causes when seasonal differences are observed, yet other factors do appear to drive seasonal changes in activity, such as access to important plant (*Meles meles*—Barrull et al. 2013) or prey resources (*M. martes*—Zielinski et al. 1983), or the care of dependent offspring (*M. foina*—Barrull et al. 2013). However, little is known about the influence of temperature and photoperiod on mustelid activity in tropical and subtropical environments, where both factors demonstrate much less variation on a daily and annual scale.

Although little studied in mustelids, there is ample evidence that many other species, particularly but not limited to those actively hunted or persecuted by humans, will alter patterns of activity to avoid times when humans are most active (Gaynor et al. 2018). Shifts to heightened activity at night, when humans are less active, are more pronounced where human disturbance

(including hunting, and proximity to settlement or infrastructure) is highest (Gaynor et al. 2018). While much of this literature has focused on larger mammals, primarily ungulates and larger carnivores, there also is evidence that mustelids and their relatives may show a similar response under varying levels of anthropogenic pressure (*Lontra longicaudis*—Rheingantz et al. 2016; *Conepatus chinga*—Castillo et al. 2014).

Whereas most research into the activity of terrestrial carnivores has relied on radiotracking of a relatively small number of individuals in a given study area, camera traps now allow us to describe activity of a species in a noninvasive and efficient manner, often gathering data from many different individuals. The dramatic increase in the number of camera-trap studies conducted across the globe (Burton et al. 2015; Wearn and Glover-Kapfer 2017) has provided a unique additional opportunity to investigate previously intractable (but see Theuerkauf 2009) questions about variation in activity across large geographic areas and the factors that may explain it (e.g., Norris et al. 2010; Gaynor et al. 2018; Lara-Díaz et al. 2018). Although camera-based data may not provide the context of potentially important intrinsic factors known to influence activity, such as sex (Zalewski 2000; Marcelli et al. 2003; Melero et al. 2011) and reproductive season or status (Leonard 1980; Arthur and Krohn 1991; Posillico et al. 1995; Jędrzejewski et al. 2000), these details are traded for the wider breadth of individuals and geographic coverage facilitated by this method.

The tayra (*Eira barbara*) is a Neotropical mustelid with a broad geographic distribution from the coasts of central Mexico to northern Argentina (Presley 2000). Few studies have documented the activity pattern of tayra in detail, but those that have describe a primarily diurnal pattern, often with peaks of activity in the early morning and late afternoon (Konecny 1989; Sunquist et al. 1989; González-Maya et al. 2015). Observations of nocturnal activity, such as movement across open areas (Defler 1980) and some sexual activity (Kaufmann and Kaufmann 1965) have been observed, but these appear to be rare. In zones with anthropogenic disturbance, tayras may be more crepuscular (Konecny 1989), but they generally remain resilient in at least some human-altered landscapes (Pardo-Vargas et al. 2016). On a seasonal basis, overall level of activity (Gonzalez-Maya et al. 2015) and the degree of diurnality (Albanesi et al. 2016) both have been shown to vary between dry and rainy seasons, with reduced midday activity during the drier, hotter periods. Sources of predation on tayra are poorly documented and the species is not commonly hunted, either on a commercial or subsistence level (Presley 2000). Tayras themselves are considered opportunistic omnivores, with reports suggesting they consume a wide variety of fruits, small vertebrates, and invertebrates (Galef et al. 1976; Presley 2000).

In this study, we describe and compare the activity patterns of populations of tayras across their distributional range in the Neotropics using a large camera-trap data set. Although our study was largely descriptive, and designed to address a lack of range-wide information on the activity of this species, the large geographic size of the tayra distribution and our collective sample sites allowed testing of hypotheses about the factors influencing activity in the species at both a spatial and temporal scale. Specifically, we attempted to use a set of biotic (human

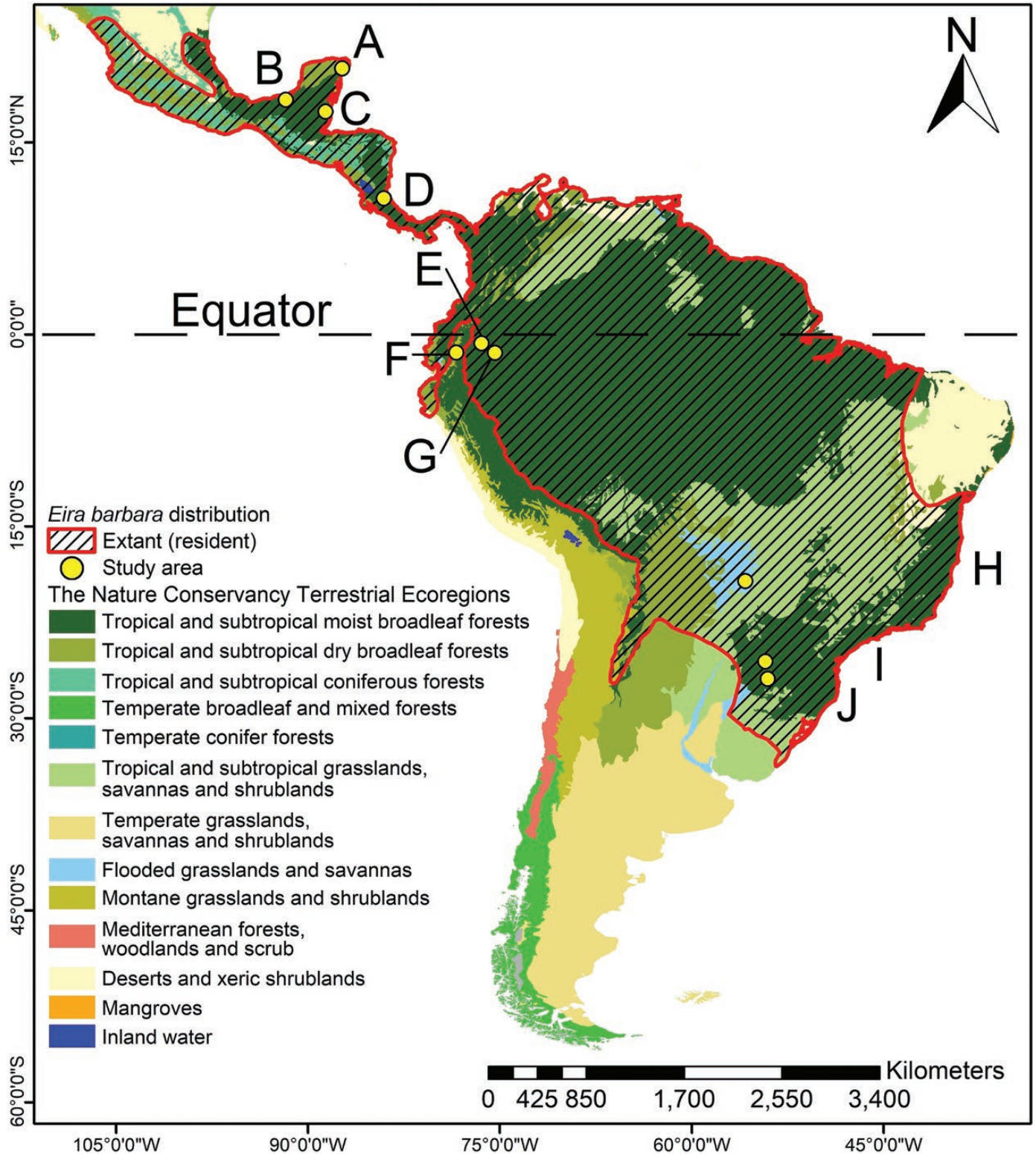
population density, vegetation greenness) and abiotic (photoperiod, temperature) variables to explain any observed variation in the level of tayra diurnality.

We hypothesized that tayra would reduce diurnality as a mechanism to reduce interactions with humans and predicted that diurnality would decline as human population density of study areas increased. We further hypothesized that reduced diurnality would be observed where individuals behaviorally avoid the risk of heat stress during the hottest hours of the day. Given the elevated risk of heat stress associated with more fragmented, hot and dry environments (Stoner and Timm 2011), we predicted that tayra would reduce diurnality where temperatures were highest and where vegetation greenness was lowest, with greenness here used as an index to level of canopy closure and overall available moisture. Because photoperiod has been shown to influence activity in other mustelids on a seasonal basis in temperate systems (see above), we investigate its influence here. However, with much less variation in this factor across the tropics, we did not hypothesize a strong influence on diurnality. Both photoperiod and daily temperature are expected to vary along a latitudinal gradient, which accounts for a suite of other climate- and habitat-related parameters not measured in our study. We therefore also investigated the relationship between latitude and level of diurnality. While not informative from an explanatory perspective, an association with latitude might serve as a proxy and offer insight into potential sources of variation in diurnality not included in our investigation.

Finally, we compared activity patterns within single sites between the rainy and the dry seasons when sampling was repeated across seasons. Previous documentation of seasonal variation in tayra activity speculated change resulted from seasonal variation both in climate and food availability and showed reduced midday activity in the dry season (Gonzalez-Maya et al. 2015). We therefore hypothesized that tayra would avoid activity during the hottest times of the day, and predicted reduced midday activity during times of year when temperatures were highest. Because this is the first description of tayra activity across its distribution and given previous evidence of diel plasticity from single sites, we expected to document variation in activity at spatial and temporal scales and offer novel insights into its potential cause.

## MATERIALS AND METHODS

**Study area.**—We obtained photographic records of tayras from 10 study areas throughout the species' range from Mexico to Argentina (Fig. 1). These study areas were those from which adequate camera-trap detection events (> 30) of tayra were collected to describe activity in the species, and whose researchers agreed to collaborate on this review. Otherwise no specific criteria were used to select study areas (Appendix I), as we hoped to use as many different study areas within the tayra distribution as possible. These areas encompassed a wide variety of biotic and abiotic conditions (Table 1). Study areas varied in elevation (0 – 3,090 m above sea level), climate seasonality (areas with a distinct dry and rainy season to areas without a



**Fig. 1.**—Study localities ( $n = 10$ ) where we detected the presence of tayra (map modified from Olson et al. 2001; Cuarón et al. 2016). Study areas: (A) Playa del Carmen (Mexico), (B) UEM Nicté-Há (Mexico), (C) Cockscomb Basin Wildlife Sanctuary (Belize), (D) San Juan-La Selva Biological Corridor (Costa Rica), (E) Yasuni Biosphere Reserve (Ecuador), (F) Ecuador Highlands (Ecuador), (G) Peruvian Amazon (Peru), (H) Baía das Pedras Ranch – El Pantanal (Brazil), (I) Iguaçu National Park (Brazil), and (J) Yaboti Biosphere Reserve (Argentina).



dry season), average annual precipitation (1,000 – 4,300 mm), and average annual temperature (12.9 – 36.9°C).

**Camera-trap data.**—The photographic records of tayra were the product of projects with various objectives focused on the study of various taxa, and only one (in Nicté-Há, Mexico, 2016 – 2017) was undertaken specifically to target tayra. For this reason, there was variation in the extent of each study area, the period of monitoring, sampling effort, and the characteristics and distribution of camera-trap stations (Table 1). However, all camera traps were functional 24 h per day and used either infrared or white flash at night. Thus, although variation in camera placement and setup likely influenced the total number of tayra records, we have no reason to believe the specific details of each study design would influence the daily timing of tayra photo records. We identified the date and hour from each tayra record. To reduce any potential biases among camera arrays, we considered consecutive images of tayra obtained at the same camera station within < 24 h to be nonindependent and therefore removed them from the data set ( $n = 29$  photos removed).

**Activity patterns.**—To compare the data from different study areas, we transformed every date to Julian day with the online software provided by the United States Naval Observatory (USNO 2018) and converted the time of each photograph to solar time using the R-package *solar* (Perpiñán Lamigueiro 2012). We used a Kernel density estimator (Ridout and Linkie 2009) to generate the activity patterns of tayras in each study area. We also pooled all the records of tayra to generate a general activity pattern of the species throughout their geographic range. Because time of sunrise and sunset varies with latitude, we calculated the average time between sunrise and sunset for each study area with the R-package *Ratmosphere* (Biavati 2014) to allow comparison among study areas. We categorized activity as: (1) diurnal, 1 h after sunrise to 1 h before sunset; (2) nocturnal, 1 h after sunset to 1 h before sunrise; and (3) crepuscular, 1 h before and after sunrise and sunset.

We compared the activity patterns of tayra between all study area pairs using the R-package *overlap* (Meredith and Ridout 2020) and calculated the overlap coefficient ( $\Delta$ ) with estimated 95% confidence intervals using a bootstrap of 10,000 samples. Following Meredith and Ridout (2020), if the smallest sample (study site in this case) has less than 50 photographic records, the  $\Delta_1$  estimator approximates the best estimates, otherwise  $\Delta_4$  is recommended in the *overlap* output. For that reason we used  $\Delta_1$  in the localities of Costa Rica, Ecuador Highlands, Peruvian Amazon, and Yaboti, and  $\Delta_4$  for the localities Playa del Carmen, Nicté-Há, Cockscomb, Yasuní, El Pantanal, and Iguacu. The estimated overlap coefficient can range from 0 (no overlap) to 1 (complete overlap). We statistically evaluated the activity patterns between pairs of study areas using the nonparametric Mardia–Watson–Wheeler test (R-package *circular*—Agostinelli and Lund 2017), to detect differences in the circular data (Batschelet 1981). This test assumes no repeat data, so identical time records on different days (captures obtained in the same hour and minute within the same study area) were altered by 1 s in the raw data.

To investigate the degree to which abiotic or biotic conditions influenced the level of diurnality of tayra across its distribution, we fitted generalized linear models (GLMs) with a binomial distribution and a proportional response variable (# of events in the day, # of events in crepuscular period) to a suite of potential predictor variables (Appendix III). Knowing the tayra to exhibit little activity during the night, we focused this analysis on determinants of diurnal behavior relative to activity near sunrise and sunset. With only 10 study sites as samples in this regression, we fitted only single-variable models to avoid overparameterization, and compared each model to an intercept-only model using an information theoretic approach and model selection via Akaike's Information Criterion corrected for small sample size (AICc—Burnham and Anderson 2002). We considered the following five predictor variables: latitude, day length, temperature, human density, and vegetation greenness (NDVI), for a total of six possible models including the null. All continuous parameters were recorded for each camera location (for the month/week they were run) from the Env-DATA platform accessed through Movebank (Dodge et al. 2013), and averaged across stations at a given study area. A  $\log_{10}$  transformation was used on the human density parameter to improve its distribution, which included large gaps between high and low values. All other parameters were modeled without transformations. Following an initial ranking of models, we checked for overdispersion (model deviance divided by residual degrees of freedom) using the highest-ranked single-variable model, because our small sample size did not allow the fully general model to be tested. We found the model to be overdispersed, and therefore reran all models and rankings using a quasibinomial distribution, which adjusts standard error estimates higher to reflect the extra-binomial variation (Zuur et al. 2009). We report summary information based on QAICc values, adjusted using a *c-hat* parameter equal to the overdispersion estimated for our highest-ranked single-variable model. We use the explained deviance (model deviance divided by null model deviance) to report the proportion of variation in diurnality explained by any single predictor variable.

In study areas with notable climatic seasonality and for which we had data from both seasons (Playa del Carmen, Nicté-Há, Cockscomb, and El Pantanal), we used the Kernel density estimator (Ridout and Linkie 2009) to generate the activity patterns of tayra separately for the dry season and the rainy season, and calculated the overlap coefficient between the seasons for each study area. Based on the number of tayra records within each season in relevant areas, we used  $\Delta_1$  estimator for the records from Playa del Carmen and Nicté-Há, and  $\Delta_4$  for Cockscomb and El Pantanal. We use the Mardia–Watson–Wheeler test, as above, to statistically compare seasonal activity patterns within sites. All statistical analyses were performed in the R environment (R Core Team 2019).

## RESULTS

We obtained 957 independent records of tayras at 10 locations in the Neotropics (Table 1). The pooled results indicated that

the majority of the tayra activity occurred during the diurnal period (79.31%, 759 records; Fig. 2) with two peaks of activity. The first peak occurred during the early hours of the morning (0900 – 1059 h), activity began to decline from 1100 h, reached the lowest diurnal point at 1300 h, and a second, lower activity peak occurred around 1500 h. Tayra also were active during crepuscular periods (18.07%, 173 records). Activity increased rapidly at sunrise and decreased more slowly by sunset. Only 2.61% (25 records) of all tayra detections occurred during the nocturnal period. The maximum proportion of nocturnal records for a study area was 6.67%, with no evidence of nocturnal activity from four of the study areas (Table 2).

While activity of tayra in the 10 localities occurred mainly during the diurnal period, we observed variation in the timing of the peaks of diurnal activity. In the study areas located in the northern hemisphere, the activity peaks in the early hours of daylight phase and in the afternoon; there was a decrease of activity around noon (Figs. 3A–D). In study areas located in the southern hemisphere near the geographical equator, tayra activity began during the early hours of the daylight phase, with a single peak of activity around noon and activity gradually decreasing thereafter (Figs. 3E–G). In the southern hemisphere study areas, activity also was diurnal, but the timing and number of activity peaks varied (Figs. 3H–J).

The overlap coefficients of tayra activity patterns varied between pairs of study sites from  $\Delta_4 = 0.69$  to  $\Delta_1 = 0.95$  (Appendix IV) with the highest overlap recorded between our two study areas located in Ecuador, and the lowest overlap between El Pantanal in Brazil and Yasuní in Ecuador. The Mardia–Watson–Wheeler results indicated that 44.44% of the activity patterns of tayra between locations were statistically different ( $P < 0.05$ ; Appendix V).

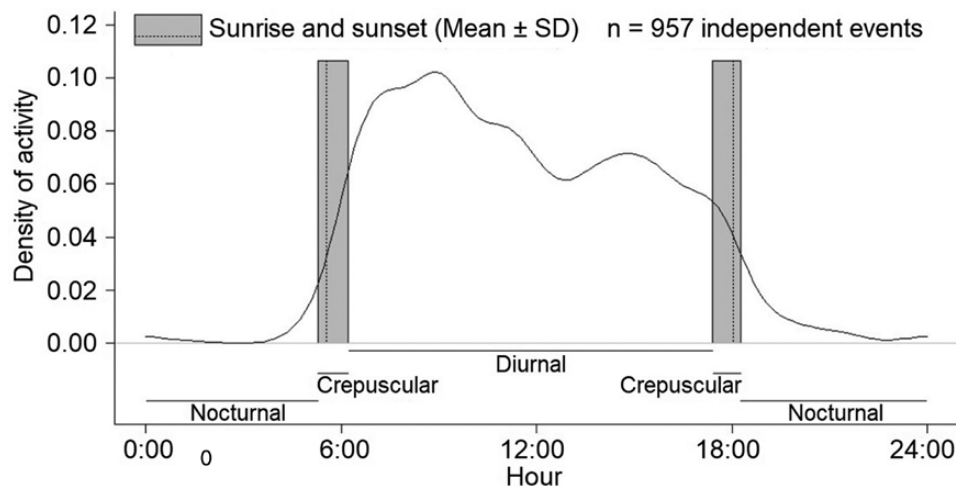
Generalized linear models based on a binomial distribution indicated that latitude was the best single-variable model (AICc weight = 0.58), yet this model was found to be overdispersed (overdispersion parameter = 2.16). We therefore proceeded to rerun all models using a quasibinomial distribution to account

for potential overdispersion, and final model rankings (Table 3) are based on QAICc values adjusted using a c-hat parameter set to 2.16. When adjusting for overdispersion, only the latitude model was ranked above the null/intercept model with a reduction in the proportion of observations in the daytime period associated with increasing distance from the equator ( $\beta = -0.051$ ,  $t = -2.376$ ,  $P = 0.045$ ; Fig. 4).

In the localities with climatic seasonality, overlap values generally were high, varying from  $\Delta_1 = 0.77$  to  $\Delta_4 = 0.90$  and overall percentages of activity in diurnal, crepuscular, and nocturnal periods were similar (Table 4; Fig. 5). In the cases of Playa del Carmen and Nigte-Há, reductions in diurnal activity of 12% and 5.3%, respectively, were found in the dry season, but overall activity patterns were not statistically different between seasons at these sites ( $X^2 = 1.68$ ,  $d.f. = 2$ ,  $P = 0.43$ ;  $X^2 = 3.25$ ,  $d.f. = 2$ ,  $P = 0.20$ ; respectively), as was the case at Cockscomb ( $X^2 = 0.77$ ,  $d.f. = 2$ ,  $P = 0.68$ ). At El Pantanal, however, there was evidence for significant differences between seasons ( $X^2 = 7.65$ ,  $d.f. = 2$ ,  $P = 0.02$ ), where the morning peak of activity was shifted closer to sunrise in the dry season.

## DISCUSSION

Our results support the notion that tayras exhibit diurnal habits throughout their distribution. Despite variation in abiotic and biotic factors across these study areas, the majority of activity (overall = 79.31%; range: 70.33% to 96.15%) occurred during daylight, with a lower proportion during crepuscular periods (18.07%; range: 0% to 18.69% around sunrise and from 3.85% to 13.33% around sunset). Although none of the specific factors that we investigated were associated strongly with the level of diurnality in the tayra, latitude explained 44% of the variation in this metric. Whereas we expected to explain variation in diurnality with variables more directly related to conditions experienced by tayra (e.g., temperature, photoperiod), the lack of importance of these other measured factors makes it challenging to explain the mechanism underlying the albeit



**Fig. 2.**—General activity pattern of tayra throughout its distribution, estimated through a kernel density function that measures the probability of observing the animal during categorized periods throughout the day. Details of assignment hours to each category are in the text.

**Table 2.**—Percentage of tayra camera-trap detections during three diel categories at 10 sites across its geographic distribution.

Country	Study area	Number of photo records	Latitudinal location*	Percentage of detections		
				Diurnal	Nocturnal	Crepuscular
Mexico	Playa del Carmen	81	20.76	76.54%	2.47%	12.35%
	UEM Nicté-Há	74	18.22	81.08%	4.05%	6.76%
Belize	Cockscomb Basin Wildlife Sanctuary	189	17.02	85.19%	2.12%	6.35%
Costa Rica	San Juan-La Selva Biological Corridor	33	10.50	84.85%	0	9.09%
	Yasuni Biosphere Reserve	52	-0.88	96.15%	0	0
Ecuador	Ecuador Highlands	35	-0.95	94.29%	0	3.85%
Peru	Peruvian Amazon	35	-1.80	94.29%	0	5.71%
Brazil	Baía das Pedras Ranch	337	-19.30	70.33%	3.86%	18.69%
	Iguaçu National Park	76	-25.53	84.21%	1.32%	3.95%
Argentina	Yaboti Biosphere Reserve	45	-26.91	75.56%	6.67%	13.33%
	Total continental ( $n = 957$ )			79.31%	2.61%	10.34%

\* = decimal degrees.

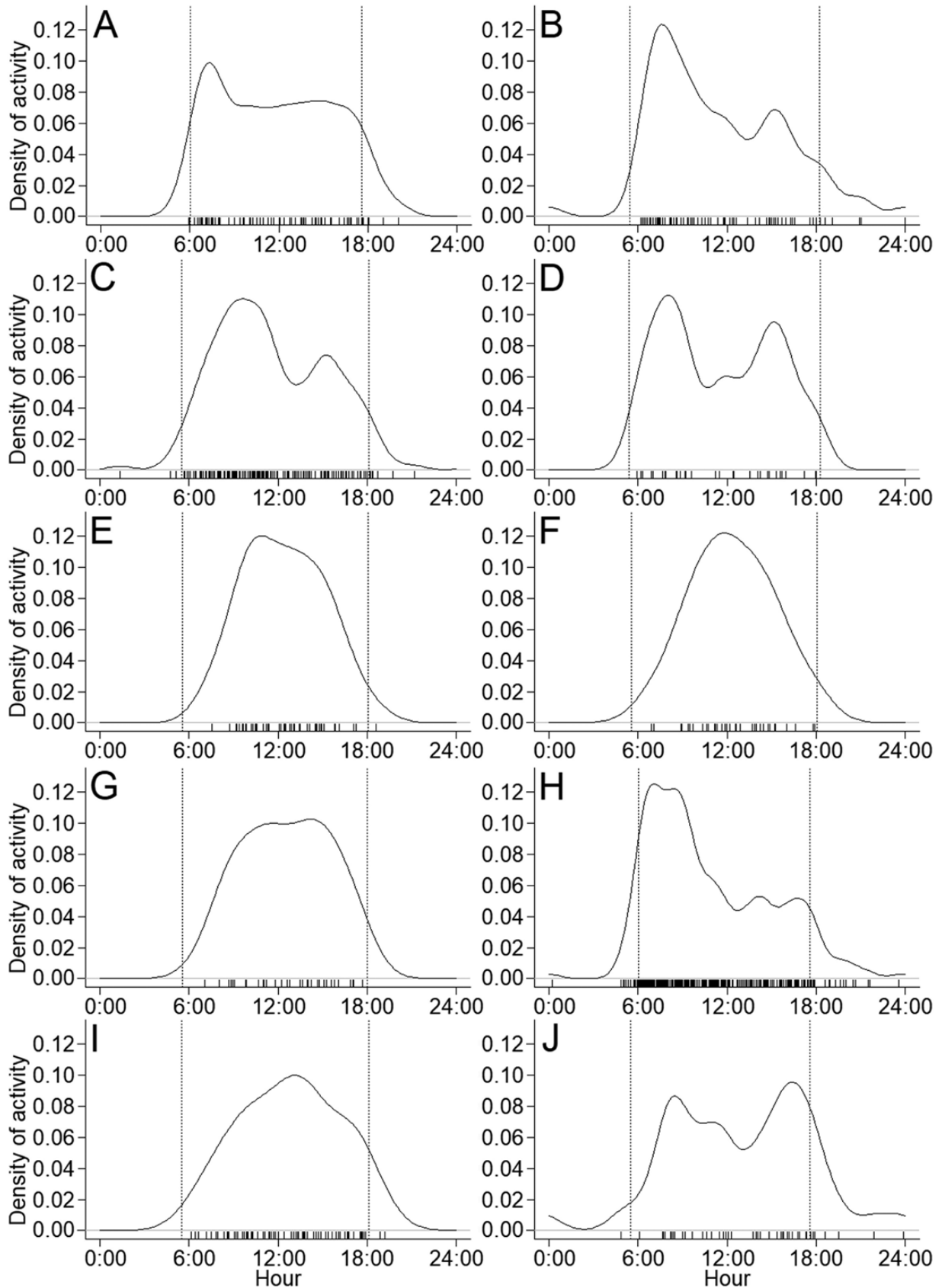
weak relationship between latitude and variation in diurnality. Whereas latitude is mechanistically related to photoperiod and temperature, these covariates were not correlated with latitude in our data set, likely owing to variation in the timing and specific location of our study areas. The role of latitude here presumably is driven by some other untested factor to which the tayra are responding. Regardless of these factors, the tayra clearly is a diurnal animal with some variation in the level of diurnality, but little nocturnal or crepuscular activity across all sites. This contradiction to observations from temperate mustelid studies documenting diel activity shifts (e.g., Zielinski et al. 1983) could be related to the broad diet of tayras not requiring a shift to track prey, particularly given the prevalence of fruit in their diets compared to other mustelids.

Although daily temperature and vegetation greenness were not supported factors predicting degree of diurnality in our regression analyses, thermal constraints acting through site-specific habitat structure (which we were unable to assess) could explain observed variation in the density of tayra activity around midday among our study areas. For example, relative declines in midday activity were observed in seasonal dry forest and fragmented forest environments (e.g., Nicté-Há and San Juan-La Selva) where tayra may be exposed to more physiologically stressful midday conditions owing to inconsistency in the forest canopy (Arroyo-Rodríguez et al. 2017). In contiguous core tropical forest environments (e.g., Yasuní Biosphere Reserve, Ecuador Highlands, and Peruvian Amazon), dense canopy cover, vegetation cover, and high humidity might provide more tolerable midday conditions. Unfortunately, this resolution of canopy fragmentation is not likely to have been represented by our metric for greenness, recorded and averaged across only camera locations, and therefore requires further investigation.

We observed midday reduction in tayra activity in half of the localities (four of them highly seasonal), which are located 10 – 26 decimal degrees from the equator. We observed an increase in activity around noon in three study areas located less than two decimal degrees from the equator. These results contrast with previous work that suggests tayra exhibit peaks of activity in the early morning and late afternoon, but nevertheless those results were obtained by different methods: direct observations (Kaufmann and Kaufmann 1965; Defler 1980) and radiotelemetry (Konecny 1989; Sunquist et al. 1989). We suggest that these current observations may be associated with the lack of marked seasonality at lower latitudes. For example, precipitation in Yasuní remains high year-round (> 100 mm/month—Valencia et al. 2004), resulting in few physiologically stressful conditions that would limit or interrupt the activity of tayra during daylight hours.

Whereas photoperiod plays a strong role in determining the seasonal activity levels and patterns of mustelids (Gerell 1969; Niemimaa 1995; Posillico et al. 1995), this association only has been investigated in temperate regions, where photoperiod varies dramatically across the year and also is associated with similarly large changes in temperature. Across our 10 study areas, photoperiod only ranged from 1029 to 1346 h, providing

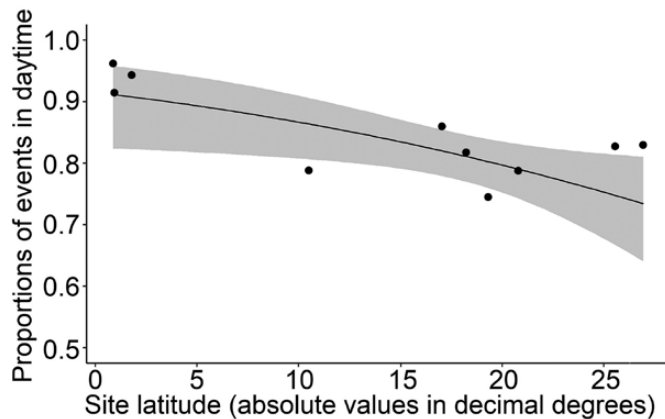




**Fig. 3.**—Activity patterns, based on kernel density estimation, of tayra in 10 study areas: (A) Playa del Carmen (Mexico), (B) UEM Nicté-Há (Mexico), (C) Cockscomb Basin Wildlife Sanctuary (Belize), (D) San Juan-La Selva Biological Corridor (Costa Rica), (E) Yasuni Biosphere Reserve (Ecuador), (F) Ecuador Highlands (Ecuador), (G) Peruvian Amazon (Peru), (H) Baía das Pedras Ranch (Brazil), (I) Iguazu National Park (Brazil), and (J) Yaboti Biosphere Reserve (Argentina). The vertical dashed lines represent the mean time of sunrise and sunset, and each record is represented as vertical ticks at the bottom of each figure.

**Table 3.**—Model selection summary for quasibinomial generalized linear model on a set of five variables predicting the proportion of diurnal activity (relative to crepuscular activity) of tayras (*Eira barbara*) from 10 study areas across the Neotropics. A  $c$ -hat adjustment of 2.16 was used to derive the QAICc values.

Model	Number of parameters	QAICc	Delta QAICc	Model likelihood	QAICc weight	Quasi-log-likelihood
Latitude	3	36.05	0.00	1.00	0.58	−13.03
Intercept-only	2	38.10	2.05	0.36	0.21	−16.20
Day length	3	38.92	2.86	0.24	0.14	−14.46
Temperature	3	42.14	6.09	0.048	0.03	−16.07
Vegetation greenness	3	42.16	6.11	0.05	0.03	−16.08
Human density	3	42.35	6.30	0.04	0.02	−16.17



**Fig. 4.**—Variation in the proportion of diurnal activity of tayra (relative to crepuscular activity) with latitudinal distance from the geographical equator based on a proportional binomial generalized linear model with only latitude as a predictor.

little variation to investigate; its relationship to temperature at this spatial scale is less obvious. We therefore expected the lack of association between photoperiod and tayra diurnality that we documented.

Although increased levels of human disturbance have caused reduced diurnality in a range of species (e.g., Frid and Dill 2002; Di Bitetti et al. 2008; Paviolo et al. 2009; Huijbers et al. 2013), we found no relationship between level of diurnality and estimated human population density. While this may indicate a certain level of resilience to human presence/activity in this species (as observed spatially in Pardo-Vargas et al. 2016), our study areas generally were not exposed to high levels of human activity, and given this fact, we were unable to sample the full range of human activity to which tayra might be exposed throughout its distribution.

Initially, we had hoped to examine the role of predation pressure in affecting tayra activity patterns. However, information on the predators of tayra is scarce; to our knowledge, tayra have been identified as prey in only one study of ocelot (*Leopardus pardalis*) diet (Bianchi et al. 2010), one study of jaguar diet (Crawshaw 1995), in the diet of harpy eagle (*Harpia harpyja*—Ferguson-Lees and Christie 2001; Aguiar-Silva et al. 2017), and presumably in the diet of puma (*Puma concolor*), given their size and similar interspecific killing (Palomares and Caro 1999). The level of potential nonlethal harassment of tayra by these other species, which also could influence tayra activity, is not known. Both jaguar

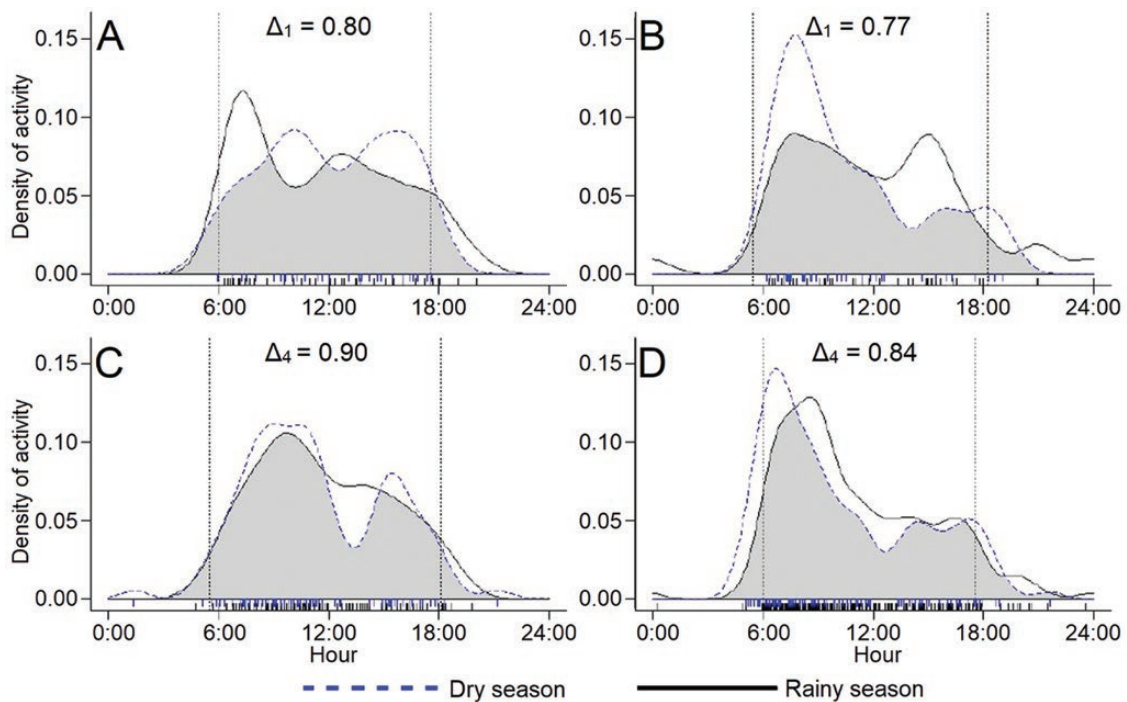
and puma are known to exhibit widely variable activity patterns across their range (e.g., Maffei et al. 2004; Blake et al. 2014; Harmsen et al. 2017), ocelots are primarily nocturnal (Sunquist and Sunquist 2002), and harpy eagles are diurnal. A robust investigation would require fully documenting the relative abundance and associated activity of each of these predators from each study area, and comparing their overlap with tayra; however, sufficient data for these predators were not available to create activity patterns in all 10 study areas. Similar challenges prevented investigation of the influence of feral and free-roaming dogs (*Canis familiaris*). Although dogs harass several wildlife species, their presence in unfragmented areas apparently is limited to their edges, and presence inside forests often is with hunters (Koster 2008). Dogs in general appear unlikely to exert strong negative effects on tayra (Koster 2008; Espartosa 2009; Lacerda et al. 2009).

In the localities with distinct dry and rainy seasons, we observed high seasonal overlap coefficients ( $> 0.70$ ), which indicate only minor variation in activity patterns across seasons. Albeit in some cases small, we observed an increase in diurnal activity during the rainy season (except for Cockscomb). These results are similar to those reported in the literature, which indicate that tayras have different activity patterns between the dry season and the rainy season (González-Maya et al. 2015; Albanesi et al. 2016). In Colombia, González-Maya et al. (2015) reported dry season peaks of activity in the first hours of morning (0800–1000 h), whereas in rainy season, activity peaked in the late afternoon. González-Maya et al. (2015) suggested that the variability of the activity patterns of tayra between seasons could be related to habitat characteristics, availability of resources such as food and water sources, and climatic constraints. In Argentina, Albanesi et al. (2016) reported the activity of tayra varied between seasons. Tayra were less active in the diurnal period during the dry season (74%) compared to the rainy season (82.2%). The increase in activity during the rainy season was not exclusive of tayra, and was observed in other species (e.g., *Nasua nasua*, *Dasyprocta punctata*, *Tapirus terrestris*, *Sylvilagus brasiliensis*, *L. pardalis*, *Pecari tajacu*, and *Cerdocyon thous*). These corresponding activity shifts in the broader mammalian community suggest that activity pattern shifts could be driven by availability of resources, hence species partitioning. However, teasing apart these ecological interactions requires additional natural history research into tayra behavior and basic ecology.

Our data come from a variety of independent studies, which presumably have different tayra densities and this affected

**Table 4.**—Activity patterns of tayra in localities where seasonality was investigated including sample size, and the percentage of detections in each period of the day.

Country	Study area	Number of photo records	Percentage of detections				
			Diurnal	Nocturnal	Crepuscular		
					Sunrise	Sunset	
Mexico	Playa del Carmen						
	Dry season	49	69.38%	2.04%	16.32%	12.24%	
	Rainy season	32	81.25%	0	9.37%	9.37%	
	UEM Nicté-Há						
Belize	Dry season	40	80.00%	7.50%	7.50%	5.00%	
	Rainy season	34	85.29%	0	5.88%	8.82%	
	Cockscomb Basin Wildlife Sanctuary						
	Dry season	109	84.40%	1.83%	7.33%	6.42%	
Brazil	Rainy season	80	83.75%	2.50%	7.50%	6.25%	
	Baía das Pedras Ranch, El Pantanal						
	Dry season	236	69.91%	5.50%	17.79%	6.77%	
	Rainy season	101	73.26%	0.99%	16.83%	8.91%	

**Fig. 5.**—Activity pattern of tayra in study areas with climatic seasonality. The vertical dashed lines represent the mean time of sunrise and sunset. A = Playa del Carmen (Mexico), B = UEM Nicté-Há (Mexico), C = Cockscomb Basin Wildlife Sanctuary (Belize), D = Baía das Pedras Ranch – El Pantanal (Brazil).

the sample sizes from these surveys. Some of these sample sizes are lower than the recommendations of 100 samples put forth by Lashley et al. (2018), but we note that our observed patterns follow our a priori expected tayra activity patterns. While we recognize that making conclusions based on the activity patterns from low samples sizes must be done with caution, we suggest that the consistency of patterns across the data sets and the lack of regression model support for sample size effects, indicates that our data sets adequately described the overall patterns of tayra activity across these regions. Furthermore, accumulating substantial activity pattern information from a vast geographic range for a relatively

low-density carnivore like the tayra represents a significant data set, and presented a unique opportunity to investigate potential large-scale patterns in activity variation, despite these limitations.

This research contributes important information about the activity patterns of tayra across their range, which represents progress in our broader understanding of the species. We demonstrated that the level of diurnality and timing of peaks of activity of the tayra vary across the distribution, as well as across seasons. This variation might reflect behavioral plasticity, which might allow tayras to succeed across a large geographic distribution. However, it remains unclear which

specific abiotic or biotic factors are driving this variation. Unfortunately, to fully separate even a few of these factors, a study would require data from 40 to 50 study areas. Large-scale camera-trapping efforts, particularly those that seek to combine survey data from numerous institutions, including Wildlife Insights (<https://wildlifeinsights.org>—Ahumada et al. 2019), will increase our ability to answer these broad-scale questions for a wide range of species, and we encourage their use to increase our understanding of how activity patterns may vary over time and space within species.

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### LITERATURE CITED

- AGOSTINELLI, C., AND U. LUND. 2017. R package ‘circular’. <https://r-forge.r-project.org/projects/circular/>. Accessed 1 February 2018.
- AGUIAR-SILVA, F. H., O. JAUDOIN, T. M. SANAIOTTI, G. H. F. SEIXAS, S. DULEBA, AND F. D. MARTINS. 2017. Camera trapping at harpy eagle nests: interspecies interactions under predation risk. *Journal of Raptor Research* 51:72–78.
- AHUMADA, J. A., ET AL. 2019. Wildlife Insights: a platform to maximize the potential of camera trap and other passive sensor wildlife data for the planet. *Environmental Conservation* 47:1–6.
- ALBANESI, S. A., J. P. JAYAT, AND A. D. BROWN. 2016. Patrones de actividad de mamíferos de medio y gran porte en el pedemonte de Yungas del noroeste Argentino. *Mastozoología Neotropical* 23:335–358.
- ARROYO-RODRÍGUEZ, V., R. A. SALDAÑA-VÁZQUEZ, L. FAHRIG, AND B. A. SANTOS. 2017. Does forest fragmentation cause an increase in forest temperature? *Ecological Research* 32:81–88.
- ARTHUR, S. M., AND W. B. KROHN. 1991. Activity patterns, movements, and reproductive ecology of fishers in southcentral Maine. *Journal of Mammalogy* 72:379–385.
- ASCHOFF, J. 1966. Circadian activity pattern with two peaks. *Ecology* 47:657–662.
- BARRULL, J., I. MATE, J. RUIZ-OLMO, J. G. CASANOVAS, J. GOSÁLBEZ, AND M. SALICRÚ. 2013. Factors and mechanisms that explain coexistence in a Mediterranean carnivore assemblage: an integrated study based on camera trapping and diet. *Mammalian Biology* 79:123–131.
- BATSCHLET, E. 1981. *Circular statistics in biology (mathematics in biology)*. 1st ed. Academic Press. New York, New York.
- BIANCHI, R. DE C., S. L. MENDES, AND P. D. M. JÚNIOR. 2010. Food habits of the ocelot, *Leopardus pardalis*, in two areas in southeast Brazil. *Studies on Neotropical Fauna and Environment* 45:111–119.
- BIAVATI, G. 2014. Standard atmospheric profiles - package ‘RAtmosphere’. <https://mran.microsoft.com/snapshot/2017-01-06/web/packages/RAtmosphere/index.html>. Accessed 1 February 2018.
- BLAKE, J. G., D. MOSQUERA, J. GUERRA, B. A. LOISELLE, D. ROMO, AND K. SWING. 2014. Yasuní – a hotspot for jaguars *Panthera onca* (Carnivora: Felidae)? Camera-traps and jaguar activity

- at Tiputini Biodiversity Station, Ecuador. *Revista de Biología Tropical* 62:689–698.
- BURNHAM, K. P., AND D. R. ANDERSON. 2002. Model selection and multimodel inference: a practical information-theoretic approach. 2nd ed. Springer. New York, New York.
- BURTON, A. C., ET AL. 2015. Review: wildlife camera trapping: a review and recommendations for linking surveys to ecological processes. *Journal of Applied Ecology* 52:675–685.
- CASTILLO, D. F., E. M. LUENGOS VIDAL, N. C. CARUSO, E. B. CASANAVE, AND M. LUCHERINI. 2014. Activity patterns of Molina's hog-nosed skunk in two areas of the Pampas grassland (Argentina) under different anthropogenic pressure. *Ethology Ecology & Evolution* 27:379–388.
- COVE, M. V., R. M. SPÍNOLA, V. L. JACKSON, AND J. C. SAÉNZ. 2014. The role of fragmentation and landscape changes in the ecological release of common nest predators in the Neotropics. *PeerJ* 2:e464.
- CRAWSHAW, P. G., JR. 1995. Comparative ecology of ocelot (*Felis pardalis*) and jaguar (*Panthera onca*) in a protected subtropical forest in Brazil and Argentina. Ph.D. dissertation, University of Florida. Gainesville, Florida.
- CUARÓN, A. D., F. REID, K. HELGEN, AND J. F. GONZÁLEZ-MAYA. 2016. *Eira barbara*. The IUCN Red List of Threatened Species 2016: e.T41644A45212151. doi:10.2305/IUCN.UK.2016-1.RLTS.T41644A45212151.en.
- DAAN, S. 1981. Adaptive daily strategies in behavior. Pp. 275–298 in *Biological rhythms* (J. Aschoff, ed.). Springer US. Boston, Massachusetts.
- DEFLER, T. R. 1980. Notes on interactions between the tayra (*Eira barbara*) and the white-fronted capuchin (*Cebus albifrons*). *Journal of Mammalogy* 61:156–156.
- DI BITETTI, M. S. D., A. PAVIOLO, C. A. FERRARI, C. D. ANGELO, AND Y. D. BLANCO. 2008. Differential responses to hunting in two sympatric species of brocket deer (*Mazama americana* and *M. nana*). *Biotropica* 40:636–645.
- DODGE, S., ET AL. 2013. The environmental-data automated track annotation (Env-DATA) system: linking animal tracks with environmental data. *Movement Ecology* 1:3.
- ESPARTOSA, K. D. 2009. Mamíferos terrestres de maior porte e a invasão de cães domésticos em remanescentes de uma paisagem fragmentada de Mata Atlântica: avaliação da eficiência de métodos de amostragem e da importância de múltiplos fatores sobre a distribuição das espécies. M.S. thesis, Universidade de São Paulo. São Paulo, Brazil.
- ESPINOSA, S. R. A. 2012. Road development, bushmeat extraction and jaguar conservation in Yasuni Biosphere Reserve - Ecuador. Ph.D. dissertation, University of Florida. Gainesville, Florida.
- ESPINOSA, S., G. CELIS, AND L. C. BRANCH. 2018. When roads appear jaguars decline: increased access to an Amazonian wilderness area reduces potential for jaguar conservation. *PLoS ONE* 13:e0189740.
- FERGUSON-LEES, J., AND D. A. CHRISTIE. 2001. Harpy eagle. Pp. 717–719 in *Raptors of the world* (J. Ferguson-Lees and D. A. Christie, eds.). Houghton Mifflin Harcourt. London, United Kingdom.
- FERNANDEZ, C. M., M. D. VERA ALVAREZ, AND M. V. COVE. 2019. Heightened nest loss in tropical forest fragments despite higher predator load in core forest. *Tropical Ecology* 60:281–287.
- FICK, S. E., AND R. J. HIJMANS. 2017. WorldClim 2: new 1-km spatial resolution climate surfaces for global land areas. *International Journal of Climatology* 37:4302–4315.
- FRID, A., AND L. M. DILL. 2002. Human-caused disturbance stimuli as a form of predation risk. *Conservation Ecology* 6:11.
- GALEF, B. G., R. A. MITTERMEIER, AND R. C. BAILEY. 1976. Predation by the tayra (*Eira barbara*). *Journal of Mammalogy* 57:760–761.
- GARCÍA, P., I. MATEOS, AND V. ARÉVALO. 2009. Diurnal activity of the American mink (*Neovison vison*) in Central Spain. *Hystrix, the Italian Journal of Mammalogy* 20:61–68.
- GAYNOR, K. M., C. E. HOJNOWSKI, N. H. CARTER, AND J. S. BRASHARES. 2018. The influence of human disturbance on wildlife nocturnality. *Science* 360:1232–1235.
- GERELL, R. 1969. Activity patterns of the mink *Mustela vison* Schreber in Southern Sweden. *Oikos* 20:451.
- GONZÁLEZ-GALLINA, A. 2018. Ecología espacial del jaguar y su relación con un proyecto carretero en el noreste de Quintana Roo. Ph.D. dissertation, Instituto de Ecología A.C. Veracruz, México.
- GONZÁLEZ-MAYA, J. F., D. ZÁRRATE-CHARRY, I. M. VELA-VARGAS, J. S. JIMÉNEZ-ALVARADO, AND D. GÓMEZ-HOYOS. 2015. Activity patterns of tayra *Eira barbara* populations from Costa Rica and Colombia: evidence of seasonal effects. *Biodiversidad Neotropical* 5:96–104.
- GRASSMAN, L. I., M. E. TEWES, AND N. J. SILVY. 2005. Ranging, habitat use and activity patterns of binturong *Arctictis binturong* and yellow-throated marten *Martes flavigula* in north-central Thailand. *Wildlife Biology* 11:49–57.
- GUERRA-SANTOS, J. J., AND J. D. W. KAHL. 2018. Redefining the seasons in the Términos Lagoon region of southeastern México: May is a transition month, not a dry month. *Journal of Coastal Research* 34:193–201.
- HARMSEN, B. J., ET AL. 2017. Long term monitoring of jaguars in the Cockscomb Basin Wildlife Sanctuary, Belize; implications for camera trap studies of carnivores. *PLoS ONE* 12:e0179505.
- HIDALGO-MIHART, M. G., ET AL. 2017. Range extension of the eastern cottontail rabbit (*Sylvilagus floridanus*) in Quintana Roo, Mexico. *Western North American Naturalist* 77:540–544.
- HIDALGO-MIHART, M. G., ET AL. 2019. Jaguar density in a mosaic of disturbed/preserved areas in southeastern Mexico. *Mammalian Biology* 98:173–178.
- HUIJBERS, C. M., T. A. SCHLACHER, D. S. SCHOEMAN, M. A. WESTON, AND R. M. CONNOLLY. 2013. Urbanisation alters processing of marine carrion on sandy beaches. *Landscape and Urban Planning* 119:1–8.
- JĘDRZEJEWSKI, W., B. JĘDRZEJEWSKA, K. ZUB, AND W. K. NOWAKOWSKI. 2000. Activity patterns of radio-tracked weasels *Mustela nivalis* in Białowieża National Park (E Poland). *Annales Zoologici Fennici* 37:161–168.
- KAMSTRA, J. 1987. An ecological survey of the Cockscomb Basin, Belize. M.S. thesis, York University. Toronto, Ontario, Canada.
- KAUFMANN, J. H., AND A. KAUFMANN. 1965. Observations of the behavior of tayras and grisons. *Zeitschrift für Säugetierkunde* 30:146–155.
- KOŁOWSKI, J. M., AND A. ALONSO. 2010. Density and activity patterns of ocelots (*Leopardus pardalis*) in northern Peru and the impact of oil exploration activities. *Biological Conservation* 143:917–925.
- KONECNY, M. J. 1989. Movement patterns and food habits of four sympatric carnivore species in Belize, Central America. *Advances in Neotropical Mammalogy* 1989:243–264.
- KOSTER, J. M. 2008. Hunting with dogs in Nicaragua: an optimal foraging approach. *Current Anthropology* 49:935–944.

- KOTTEK, M., J. GRIESER, C. BECK, B. RUDOLF, AND F. RUBEL. 2006. World map of the Köppen-Geiger climate classification updated. *Meteorologische Zeitschrift* 15:259–263.
- LACERDA, A. C. R., W. M. TOMAS, AND J. MARINHO-FILHO. 2009. Domestic dogs as an edge effect in the Brasília National Park, Brazil: interactions with native mammals. *Animal Conservation* 12:477–487.
- LARA-DÍAZ, N. E., H. CORONEL-ARELLANO, C. A. LÓPEZ-GONZÁLEZ, G. SÁNCHEZ-ROJAS, AND J. E. MARTÍNEZ-GÓMEZ. 2018. Activity and resource selection of a threatened carnivore: the case of black bears in northwestern Mexico. *Ecosphere* 9:e01923.
- LARIVIÈRE, S., AND A. P. JENNINGS. 2009. Family Mustelidae (American mink). Pp. 655–656 in *Handbook of the mammals of the world. 1 – carnivores* (D. E. Wilson and R. A. Mittermeier, eds.). Lynx Edicions, Barcelona, Spain.
- LASHLEY, M. A., ET AL. 2018. Estimating wildlife activity curves: comparison of methods and sample size. *Scientific Reports* 8:4173.
- LEONARD, R. D. 1980. The winter activity and movements, winter diet, and breeding biology of the fisher (*Martes pennanti*) in south-eastern Manitoba. M.S. thesis, University of Manitoba, Winnipeg, Manitoba, Canada.
- MAFFEI, L., E. CUÉLLAR, AND A. NOSS. 2004. One thousand jaguars (*Panthera onca*) in Bolivia's Chaco? Camera trapping in the Kaa-Iya National Park. *Journal of Zoology* 262:295–304.
- MAGOUN, A. J., P. VALKENBURG, AND R. E. LOWELL. 2008. Habitat associations and movement patterns of reproductive female wolverines (*Gulo gulo luscus*) on the Southeast Alaska mainland. *Wildlife Research Annual Progress Report*. Alaska Department of Fish and Game, Petersburg, Alaska.
- MARCELLI, M., R. FUSILLO, AND L. BOITANI. 2003. Sexual segregation in the activity patterns of European polecats (*Mustela putorius*). *Journal of Zoology* 261:249–255.
- MCCANN, N. P., P. A. ZOLLNER, AND J. H. GILBERT. 2019. Activity of fishers at multiple temporal scales. *Journal of Mammalogy* 100:178–184.
- MELERO, Y., S. PALAZON, E. REVILLA, AND J. GOSALBEZ. 2011. Winter activity patterns in an invading Mediterranean population of American mink (*Neovison vison*). *Folia Zoologica* 60:47–53.
- MEREDITH, M., AND M. RIDOUT. 2020. Estimates of coefficient of overlapping for animal activity patterns - package 'overlap.'
- NIEMIMAA, J. 1995. Activity patterns and home ranges of the American mink *Mustela vison* in the Finnish outer archipelago. *Finnish Zoological and Botanical Publishing Board* 32:117–121.
- NORRIS, D., F. MICHALSKI, AND C. A. PERES. 2010. Habitat patch size modulates terrestrial mammal activity patterns in Amazonian forest fragments. *Journal of Mammalogy* 91:551–560.
- OLSON, D. M., ET AL. 2001. Terrestrial ecoregions of the world: a new map of life on earth. *BioScience* 51:933–938.
- PALOMARES, F., AND T. M. CARO. 1999. Interspecific killing among mammalian carnivores. *The American Naturalist* 153:492–508.
- PARDO-VARGAS, L. E., M. V. COVE, R. M. SPINOLA, J. C. DE LA CRUZ, AND J. C. SAENZ. 2016. Assessing species traits and landscape relationships of the mammalian carnivore community in a Neotropical biological corridor. *Biodiversity and Conservation* 25:739–752.
- PAVIOLLO, A., Y. E. DI BLANCO, C. D. DE ANGELO, AND M. S. DI BITETTI. 2009. Protection affects the abundance and activity patterns of pumas in the Atlantic Forest. *Journal of Mammalogy* 90:926–934.
- PERPIÑÁN LAMIGUEIRO, O. 2012. solaR: solar radiation and photovoltaic systems with R. *Journal of Statistical Software* 50:9.
- POSILLICO, M., P. SERAFINI, AND S. LOVARI. 1995. Activity patterns of the stone marten *Martes foina* Erxleben, 1777, in relation to some environmental factors. *Hystrix, the Italian Journal of Mammalogy* 7:79–97.
- POTT, A., AND V. J. POTT. 2009. Vegetação do Pantanal: fitogeografia e dinâmica. Pp. 1065–1076 in *Anais 2o Simpósio de Geotecnologias no Pantanal, Corumba, 7–11 novembro 2009*. Embrapa Informática Agropecuária/INPE, Brasília, D.F., Brazil.
- PRESLEY, S. J. 2000. *Eira barbara*. *Mammalian Species* 636:1–6.
- R CORE TEAM. 2019. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.
- REYES-PUIG, C. P., G. D. RÍOS-ALVEAR, AND J. P. REYES-PUIG. 2015. Notable ampliación del rango altitudinal de *Eira barbara* Cabeza de Mate (Mammalia: Mustelidae). *ACI Avances en Ciencias e Ingenierías* 7:B98–B102.
- RHEINGANTZ, M. L., C. LEUCHTENBERGER, C. A. ZUCCO, AND F. A. S. FERNANDEZ. 2016. Differences in activity patterns of the Neotropical otter *Lontra longicaudis* between rivers of two Brazilian ecoregions. *Journal of Tropical Ecology* 32:170–174.
- RICHARDSON, L., T. W. CLARK, S. C. FORREST, AND T. M. CAMPBELL, III. 1987. Winter ecology of black-footed ferrets (*Mustela nigripes*) at Meeteetse, Wyoming. *American Midland Naturalist* 117:225–239.
- RIDOUT, M. S., AND M. LINKIE. 2009. Estimating overlap of daily activity patterns from camera trap data. *Journal of Agricultural, Biological, and Environmental Statistics* 14:322–337.
- RÍOS-ALVEAR, D. G. 2016. Integración de modelos de circuitos y modelos de ocupación de sitios para evaluar la conectividad de poblaciones de fauna silvestre. M.S. thesis, Pontificia Universidad Católica del Ecuador, Quito, Ecuador.
- RUSAK, B., AND Z. BOULOS. 1981. Pathways for photic entrainment of mammalian circadian rhythms. *Photochemistry and Photobiology* 34:267–273.
- STONER, K. E., AND R. M. TIMM. 2011. Seasonally dry tropical forest mammals: adaptations and seasonal patterns. Pp. 85–106 in *Seasonally dry tropical forests* (R. Dirzo, H. S. Young, H. A. Mooney, and G. Ceballos, eds.). Island Press/Center for Resource Economics, Washington, D.C.
- SUNQUIST, M., AND F. SUNQUIST. 2002. *Wild cats of the World*. University of Chicago Press, Chicago, Illinois.
- SUNQUIST, M. E., F. SUNQUIST, AND D. E. DANEKE. 1989. Ecological separation in a Venezuelan Llanos carnivore community. Pp. 197–232 in *Advances in Neotropical Mammalogy* (K. H. Redford and J. F. Eisenberg, eds.). Sandhill Crane Press, Gainesville, Florida.
- THEUERKAUF, J. 2009. What drives wolves: fear or hunger? Humans, diet, climate and wolf activity patterns. *Ethology* 115:649–657.
- UNITED STATES NAVAL OBSERVATORY. 2018. Julian date (JD) calculator and calendars | aavso.org. <https://www.aavso.org/jd-calculator>. Accessed 15 March 2019.
- VALENCIA, R., ET AL. 2004. Tree species distributions and local habitat variation in the Amazon: large forest plot in eastern Ecuador. *Journal of Ecology* 92:214–229.

- WEARN, O. R., AND P. GLOVER-KAPFER. 2017. Camera-trapping for conservation: a guide to best-practices. WWF Conservation Technology Series 1:181.
- XAVIER DA SILVA, M., A. PAVIOLO, L. R. TAMBOSI, AND R. PARDINI. 2018. Effectiveness of protected areas for biodiversity conservation: mammal occupancy patterns in the Iguacu National Park, Brazil. *Journal for Nature Conservation* 41:51–62.
- YAMAGUCHI, N., S. RUSHTON, AND D. W. MACDONALD. 2003. Habitat preferences of feral American mink in the Upper Thames. *Journal of Mammalogy* 84:1356–1373.
- ZALEWSKI, A. 2000. Factors affecting the duration of activity by pine martens (*Martes martes*) in the Białowieża National Park, Poland. *Journal of Zoology* 251:439–447.
- ZIELINSKI, W. J., W. D. SPENCER, AND R. H. BARRETT. 1983. Relationship between food habits and activity patterns of pine martens. *Journal of Mammalogy* 64:387–396.
- ZUBEROGOITIA, I., J. ZABALA, AND J. A. MARTÍNEZ. 2006. Diurnal activity and observations of the hunting and ranging behaviour of the American mink (*Mustela vison*). *Mammalia* 70:310–312.
- ZUUR, A. F., E. N. IENO, N. J. WALKER, A. A. SAVELIEV, AND G. M. SMITH. 2009. Mixed effects models and extensions in ecology with R. Springer Verlag. New York, New York.

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## APPENDIX I

Latitude, longitude (decimal degrees), and years of camera-trap surveys in each study area.

Country	Study area	Latitude	Longitude	Years of survey
Mexico	Playa del Carmen	20.76	–87.27	2012–2013
	Unit Environmental Management Nicté-Há	18.22	–91.80	2016–2017
Belize	Cockscomb Basin Wildlife Sanctuary	17.02	–88.54	2008–2009, 2011–2016
Costa Rica	San Juan-La Selva Biological Corridor	10.50	–84.13	2009–2010, 2016, 2018
Ecuador	Yasuní Biosphere Reserve	–0.88	–76.32	2007–2009
	Ecuador Highlands	–0.95	–78.09	2011–2012, 2014
Peru	Peruvian Amazon	–1.80	–75.65	2008
Brazil	Baía das Pedras Ranch, El Pantanal	–19.30	–55.79	2011–2018
	Iguaçu National Park	–25.53	–54.22	2009–2011, 2013–2014, 2016
Argentina	Yaboti Biosphere Reserve	–26.91	–53.99	2005

## APPENDIX II

Description of the camera-trap surveys in Nicté-Há, Campeche, Mexico.

The camera-trap survey conducted from 2016 to 2017 in the UEM Nicté-Há (91°43′10.21″W; 18°20′29.79″N) by ÁJV-T was specifically designed to obtain tayra records. Due to the characteristics of the vegetation, the trails that already existed within the UEM were used. The camera-trap stations placed in the same trail had a separation of 1 km. The literature reports a strong arboreal tendency in tayra (Presley 2000); for that reason the camera-trap stations were placed inside the vegetation, at a distance between 7 and 12 m from the trails.

In 2016 (from March to May) we placed 25 camera-trap stations each with a single digital infrared trail camera (Wildview, Model STC-WV40NG, Grand Prairie, Texas) at a height of approximately 25–45 cm. Each station had a partially opened sardine can at about 4 m in front of each camera, and a stick with lure to attract mustelids (only one of these lures was used per station: Mink Lure Supreme, Long Distance Call Lure, Marsyada's; Allagash Fur Call, Cronk's; Mink Master - Mink Gland Lure, Caven's; or Weasel Lure, Hawbaker's; all manufactured by Minnesota Trapline Products, Inc.). In addition, we placed six camera-trap stations composed of two digital infrared trail camera (Wildview, Model STC-WV40NG, Texas) at a height of

100–120 cm; the cameras were focused to a rig (a modification of the method used by Magoun et al. 2008) designed to obtain front and side images and external morphometric measures of the photographed specimens. The rigs were lured with a partially opened sardine can, chicken pieces, apples, bananas, honey, and one of the mentioned lures.

In 2017 (from February to May) we placed 24 camera-trap stations with a single digital infrared trail camera (Wildview, Model STC-WV40NG, Texas) at a height of approximately 25–45 cm. Each station had a partially opened sardine can at about 4 m in front of each camera, and a stick with lure to attract mustelids (Salmon Oil, Caven's, Minnesota Trapline Products, Inc.). In addition, we placed five camera-trap stations composed of two digital infrared trail camera (Browning Strike Force HD 850 Sub Micro Series, Birmingham, Alabama) at a height of 100–120 cm; the cameras were focused to a rig (with the same specifications of the 2016 survey). The rigs were lured with a partially opened sardine can, chicken pieces, apples, bananas, honey, and salmon oil.

All the camera-trap stations placed in both surveys formed a polygon of 21.73 km<sup>2</sup>. The cameras functioned continuously 24 h/day, and were checked every 25–28 days to replace memory cards and batteries. It is considered a single camera-day when the camera trap functioned adequately for uninterrupted periods of 24 h.

## APPENDIX III

Sources and details for covariate set used in regression analysis predicting level of diurnality in tayra across their geographic range.

Covariate	Description	Unit	Interpolation	Spatial granularity	Source	Provider
Human density*	Human population densities in 2000	Persons/km <sup>2</sup>	Bilinear	30 arc-second	SEDAC GPW V3 and GRUMP V1 GRUMP 2000 Population Density Adjusted	CIESIN at Columbia University
Temperature*	Daily air temperature 2 m above ground	Degrees C	Bilinear	0.75 degrees	ECMWF Interim Full Daily SFC Temperature (2 m above ground)	European Centre for Medium-Range Weather Forecasts
Vegetation greenness*	NDVI	NA	Bilinear	250 m	MODIS Land Vegetation Indices 250-m 16-d Aqua NDVI	NASA Land Processes Distributed Active Archive Center
Sample size	Number of tayra records obtained in each study area during the survey	Quantitative	N/A	N/A	Directly assessed from raw camera-trap data files	N/A
Latitude	Latitudinal location of each record of tayra used in this study	Decimal degrees	N/A	N/A	Coordinates provided by coauthors	N/A
Photoperiod	Quantity of hours with light	Hours	N/A	N/A	Calculated with R-package Ratmosphere	N/A

CIESIN = Center for International Earth Science Information Network; ECMWF = European Centre for Medium-Range Weather Forecasts; GPW = Gridded Population of the World; GRUMP = Global Rural-Urban Mapping Project; MODIS = Moderate Resolution Imaging Spectroradiometer; N/A = not applicable; NASA = National Aeronautics and Space Administration; NDVI = Normalized Difference Vegetation Index; and SEDAC = Socioeconomic Data and Applications Center. \*Data were accessed via ENV-Data via Movebank ([www.movebank.org](http://www.movebank.org)—Dodge et al. 2013).

## APPENDIX IV

Overlap coefficients of the activity patterns of tayra, and latitudinal distance (in decimal degrees) between pairs of study sites, overlap coefficient in upper right cells, latitudinal distance in lower left cells.

Country	Mexico		Belize	Costa Rica	Ecuador		Peru	Brazil		Argentina
Study area	Playa del Carmen	UEM Nicté-Há	Cockscomb Basin Wildlife Sanctuary	San Juan-La Selva Biological Corridor	Yasuni Biosphere Reserve	Ecuador Highlands	Peruvian Amazon	Baía das Pedras Ranch, El Pantanal	Iguaçu National Park	Yaboti Biosphere Reserve
Playa del Carmen	—	$\Delta_4 = 0.88$	$\Delta_4 = 0.87$	$\Delta_1 = 0.90$	$\Delta_4 = 0.74$	$\Delta_1 = 0.76$	$\Delta_1 = 0.80$	$\Delta_4 = 0.83$	$\Delta_4 = 0.85$	$\Delta_1 = 0.84$
UEM Nicté-Há	2.54	—	$\Delta_4 = 0.86$	$\Delta_1 = 0.88$	$\Delta_4 = 0.69$	$\Delta_1 = 0.71$	$\Delta_1 = 0.73$	$\Delta_4 = 0.91$	$\Delta_4 = 0.74$	$\Delta_1 = 0.82$
Cockscomb Basin Wildlife Sanctuary	3.74	1.20	—	$\Delta_1 = 0.85$	$\Delta_4 = 0.80$	$\Delta_1 = 0.80$	$\Delta_1 = 0.82$	$\Delta_4 = 0.82$	$\Delta_4 = 0.82$	$\Delta_1 = 0.83$
San Juan-La Selva Biological Corridor	10.28	7.73	6.53	—	$\Delta_1 = 0.72$	$\Delta_1 = 0.73$	$\Delta_1 = 0.78$	$\Delta_1 = 0.85$	$\Delta_1 = 0.77$	$\Delta_1 = 0.80$
Yasuni Biosphere Reserve	21.64	19.10	17.90	11.36	—	$\Delta_1 = 0.95$	$\Delta_1 = 0.91$	$\Delta_4 = 0.64$	$\Delta_4 = 0.86$	$\Delta_1 = 0.71$
Ecuador Highlands	21.71	19.17	17.97	11.43	0.07	—	$\Delta_1 = 0.91$	$\Delta_1 = 0.66$	$\Delta_1 = 0.87$	$\Delta_1 = 0.72$
Peruvian Amazon	22.56	20.02	18.82	12.28	0.91	0.84	—	$\Delta_1 = 0.68$	$\Delta_1 = 0.91$	$\Delta_1 = 0.78$
Baía das Pedras Ranch, El Pantanal	40.06	37.52	36.32	29.78	18.42	18.35	17.50	—	$\Delta_4 = 0.70$	$\Delta_1 = 0.76$
Iguaçu National Park	46.30	43.76	42.55	36.02	24.65	24.58	23.73	6.23	—	$\Delta_1 = 0.84$
Yaboti Biosphere Reserve	47.68	45.13	43.93	37.40	26.03	25.96	25.11	7.61	1.37	—



## APPENDIX V

Comparison of the activity patterns/records of tayra in different locations through the Mardia–Watson–Wheeler test.

Study area ( <i>country</i> )	Compared activity area ( <i>country</i> )	Chi-square	Degrees of freedom	<i>P</i> -value		
Playa del Carmen ( <i>Mexico</i> )	UEM Nicté-Há ( <i>Mexico</i> )	2.01	2	0.37		
	Cockscomb Basin Wildlife Sanctuary ( <i>Belize</i> )	3.14	2	0.20		
	San Juan-La Selva Biological Corridor ( <i>Costa Rica</i> )	0.06	2	0.96		
	Yasuni Biosphere Reserve ( <i>Ecuador</i> )	11.56	2	< 0.05*		
	Ecuador Highlands ( <i>Ecuador</i> )	8.07	2	< 0.05*		
	Peruvian Amazon ( <i>Peru</i> )	5.05	2	0.08		
	Baía das Pedras Ranch, El Pantanal ( <i>Brazil</i> )	5.65	2	0.06		
	Iguaçu National Park ( <i>Brazil</i> )	3.9	2	0.14		
	Yaboti Biosphere Reserve ( <i>Argentina</i> )	0.28	2	0.86		
	UEM Nicté-Há ( <i>Mexico</i> )	Cockscomb Basin Wildlife Sanctuary ( <i>Belize</i> )	3.70	2	0.16	
San Juan-La Selva Biological Corridor ( <i>Costa Rica</i> )		0.52	2	0.76		
Yasuni Biosphere Reserve ( <i>Ecuador</i> )		16.22	2	< 0.001*		
Ecuador Highlands ( <i>Ecuador</i> )		12.78	2	< 0.001*		
Peruvian Amazon ( <i>Peru</i> )		9.23	2	0.01*		
Baía das Pedras Ranch, El Pantanal ( <i>Brazil</i> )		0.41	2	0.82		
Iguaçu National Park ( <i>Brazil</i> )		10.54	2	< 0.05*		
Yaboti Biosphere Reserve ( <i>Argentina</i> )		2.32	2	0.30		
Cockscomb Basin Wildlife Sanctuary ( <i>Belize</i> )		San Juan-La Selva Biological Corridor ( <i>Costa Rica</i> )	1.91	2	0.38	
		Yasuni Biosphere Reserve ( <i>Ecuador</i> )	11.79	2	< 0.05*	
	Ecuador Highlands ( <i>Ecuador</i> )	9.43	2	0.01*		
	Peruvian Amazon ( <i>Peru</i> )	5.02	2	0.08		
	Baía das Pedras Ranch, El Pantanal ( <i>Brazil</i> )	15.86	2	< 0.001*		
	Iguaçu National Park ( <i>Brazil</i> )	7.03	2	0.03*		
	Yaboti Biosphere Reserve ( <i>Argentina</i> )	4.22	2	0.12		
	San Juan-La Selva Biological Corridor ( <i>Costa Rica</i> )	Yasuni Biosphere Reserve ( <i>Ecuador</i> )	8.76	2	0.01*	
		Ecuador Highlands ( <i>Ecuador</i> )	7.94	2	0.02*	
		Peruvian Amazon ( <i>Peru</i> )	4.69	2	0.09	
Baía das Pedras Ranch, El Pantanal ( <i>Brazil</i> )		1.42	2	0.49		
Iguaçu National Park ( <i>Brazil</i> )		3.39	2	0.18		
Yaboti Biosphere Reserve ( <i>Argentina</i> )		0.57	2	0.74		
Yasuni Biosphere Reserve ( <i>Ecuador</i> )		Ecuador Highlands ( <i>Ecuador</i> )	0.06	2	0.96	
		Peruvian Amazon ( <i>Peru</i> )	0.81	2	0.66	
		Baía das Pedras Ranch, El Pantanal ( <i>Brazil</i> )	32.07	2	< 0.001*	
		Iguaçu National Park ( <i>Brazil</i> )	2.76	2	0.25	
	Yaboti Biosphere Reserve ( <i>Argentina</i> )	11.41	2	< 0.05*		
	Ecuador Highlands ( <i>Ecuador</i> )	Peruvian Amazon ( <i>Peru</i> )	0.78	2	0.67	
		Baía das Pedras Ranch, El Pantanal ( <i>Brazil</i> )	21.37	2	< 0.001*	
		Iguaçu National Park ( <i>Brazil</i> )	1.91	2	0.38	
		Yaboti Biosphere Reserve ( <i>Argentina</i> )	9.68	2	< 0.05*	
		Peruvian Amazon ( <i>Peru</i> )	Baía das Pedras Ranch, El Pantanal ( <i>Brazil</i> )	16.44	2	< 0.001*
Iguaçu National Park ( <i>Brazil</i> )			0.18	2	0.91	
Yaboti Biosphere Reserve ( <i>Argentina</i> )			6.46	2	0.04*	
Baía das Pedras Ranch, El Pantanal ( <i>Brazil</i> )			Iguaçu National Park ( <i>Brazil</i> )	26.03	2	< 0.001*
			Yaboti Biosphere Reserve ( <i>Argentina</i> )	6.79	2	0.03*
			Iguaçu National Park ( <i>Brazil</i> )	Yaboti Biosphere Reserve ( <i>Argentina</i> )	4.29	2

\* = *P*-value ≤ 0.05 indicates significant dissimilarities between the daily distributions of records.