

ORIGINAL RESEARCH

Night life: Positional behaviors and activity patterns of the Neotropical kinkajou, *Potos flavus* (Carnivora, Procyonidae)

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Abstract

Studying positional behaviors is important for understanding how animals interact with their immediate environment. This is particularly important in arboreal species since arboreal milieus are primarily characterized by three-dimensional problems that arboreal species must overcome to efficiently access resources. Similarly, a fundamental aspect of an animal's ecology is its daily activity pattern. This information is important for understanding the basic ecology of animal species and their eco-evolutionary dynamics. This study sought to understand the habitat use and nocturnal lifestyle of the highly arboreal kinkajou (*Potos flavus*) by documenting variation in positional behaviors and activity patterns using 2223 photographs obtained from 27 camera traps in French Guiana. Data were analyzed using descriptive statistics, Kernel density estimation (KDE), and Gantt charts. Our results indicate that kinkajous show a strictly nocturnal activity pattern beginning from 19:00 h to 05:57 h, with peak active periods between 01:00 h and 02:00 h. The most frequent activities were scanning (48.33%) and traveling (47.13%). Quadrupedal walking (95.43%) was the main locomotor behavior during traveling. However, when crossing gaps between two substrates, kinkajous would either bridge (42.22%), leap (33.33%), or drop (26.67%) across gaps. Inactive periods were characterized by grooming (77.32%) and resting (27.84%) while mostly assuming a sitting (90.67%) or a catlike body curl posture (92.59%), interchangeably. This study highlights the broad array of positional behaviors displayed by kinkajous, further providing information to understand its basic ecology and eco-evolutionary dynamics.

Introduction

The study of positional behavior (locomotion and posture) is a highly integrative field of research that attempts to describe movements and behaviors of animals, therefore providing a comprehensive understanding of how animals interact with their environment (Bezanson, 2017). Positional behaviors provide important information not only for untangling form–function relationships within evolutionary lineages, but also for understanding their adaptive significance in food acquisition and manipulation, predator avoidance, social interactions, and access to mating opportunities (Bezanson & Morbeck, 2013; Youlatos & Guillot, 2015). Moreover, positional behaviors also provide evidence for the biological roles of morphological

character complexes as well as relevant contextual knowledge for functional-adaptive analysis (Stafford et al., 2003).

Locomotor and postural behaviors are largely influenced by a combination of morphological features (e.g., body size) and their interaction with the immediate environment (Youlatos & Gasc, 2001). This is especially evident in arboreal animals because tree canopies are characterized by three-dimensional problems that arboreal species must constantly overcome to efficiently access food, shelter, and mating partners. More specifically, arboreal habitats are characterized by limited discontinuous supports that are variable in width, flexibility, and orientation (Youlatos et al., 2008). Such habitat variations therefore act as a potential selective force influencing diversification of morphological and behavioral adaptations, especially

among arboreal and semi-arboreal mammals. For instance, primates have evolved specialized morphological adaptations such as forelimb elongation, claw-like nails, and hind limb elongation that allow for efficient suspensory behaviors, vertical clinging, and movement on vertical supports, respectively (Zhu *et al.*, 2015). These adaptations play a critical role in habitat utilization and resource acquisition, allowing for efficient use and navigation on terminal branches through an increased grasping ability (Li *et al.*, 2022). However, previous studies trying to understand positional behaviors of arboreal mammals have focused predominantly on primates (Bezanson, 2017; Bicca-Marques & Calegari-Marques, 2008; Chatani, 2003; Li *et al.*, 2022; Wright *et al.*, 2019; Youlatos & Guillot, 2015) with little focus on the positional behaviors of non-primate arboreal mammals. Therefore, there is a need to investigate the locomotor and postural behaviors exhibited by non-primates in arboreal environments. Such information is important for unraveling the evolutionary adaptations of arboreal species (*i.e.*, both primates and non-primates), and how they use and share resources in this complex three-dimensional environment.

The study of the activity patterns also provides insights into a fundamental aspect of the ecology of an organism. While some animals are predominantly active during daytime (diurnal), others are active during the night (nocturnal), twilight (crepuscular), or even throughout the day (catheermal) (Ikeda *et al.*, 2016; Vallejo-Vargas *et al.*, 2022). Like in many animals, the activity pattern of mammals may depend on food availability, habitat structure, climate, and intra- and interspecific interactions, such as competition and predation (Ramírez-Mejía & Sánchez, 2016). For instance, rodents may display nocturnal activities to avoid diurnal predators, but may also be active during the day to exploit food resources and potentially reduce competition (Vallejo-Vargas *et al.*, 2022). As such, information on the daily activity patterns, particularly in poorly understood arboreal species, is relevant to understand species interactions from both an ecological and evolutionary perspective.

Before the advent of camera traps, studies documenting the positional behaviors and activity patterns of mammals involved direct observations. This approach not only disturbed focal populations, thus, biasing the information obtained, but also demanded high survey efforts, especially when studying enigmatic and nocturnal species, and those living in rugged terrain (Ota *et al.*, 2019). Moreover, direct observation methods can be challenging when investigating arboreal species within dense tree canopies. Given these drawbacks, the introduction of camera traps has received a great deal of attention in wildlife surveys over the past few decades. Camera traps provide a non-invasive method of accurately documenting presence and absence of multiple species together with their corresponding spatial and temporal behaviors within their natural environments (Astiazarán Azcarraga *et al.*, 2020). Camera traps have been used to document activity patterns (Blake *et al.*, 2012; Gracani & Mikac, 2022; Halle & Stenseth, 2000; Monterroso *et al.*, 2013; Ramírez-Mejía & Sánchez, 2016; Van Schaik & Griffiths, 1996) and even some positional behaviors in mammals (Daloz *et al.*, 2012). However, the application of this methodology to evaluate the locomotor and postural behaviors,

along with activity patterns remains largely understudied in enigmatic arboreal species within the canopy of dense forests.

One poorly understood forest mammal is the primate-like carnivore, the kinkajou (*Potos flavus*). The kinkajou is a medium-sized procyonid inhabiting most parts of the Neotropical forests from central to northern South America (Kays, 1999; Wright & Edwards, 2009). Its rounded head and short face, together with its frugivorous and strongly arboreal lifestyle parallels that of several primates (Kays & Gittleman, 1995). Yet, data on some aspects of its ecology, life-history traits, and evolutionary dynamics remain scant. The few studies documenting the ecology of kinkajous have primarily focused on their home range (Julien-Laferrière, 1993), social organization (Kays *et al.*, 2000; Kays & Gittleman, 2001), and dietary behavior (Julien-Laferrière, 2001; Séguigne *et al.*, 2022). Nevertheless, other fundamental aspects of their ecology and behavior, particularly locomotor and postural behaviors as well as their activity patterns remain understudied. The present study therefore investigated aspects of the positional behaviors and general activity patterns of kinkajous located within the rainforest of French Guiana. Our data are important to better understand the basic ecology (*e.g.*, species-environment interactions) and eco-evolutionary dynamics, such as interspecific competition, predator-prey interactions, and spatio-temporal niche partitioning and segregation between the study species and other sympatric species (*e.g.*, *Alouatta macconnelli*, *Sapajus apella*, *Ateles paniscus*).

Materials and methods

Study area

The study was conducted in the rainforest of French Guiana, specifically along the mature rainforest of the “Nationale 2” road extending from Cayenne to Saint-Georges-de-l’Oyapock (near Oyapock River), which makes up the border between Brazil and French Guiana (Fig. 1). The area is characterized by hilltop and downslope forests, both of which present a different species composition (Guitet *et al.*, 2015). The forest is a mosaic of mixed forest types and ecotones (Coutant *et al.*, 2022) with altitudes ranging between 30 and 90 m above sea level (Séguigne *et al.*, 2022). It has a humid equatorial climate characterized by a mean temperature of about 26°C and a mean annual rainfall of about 2861 mm per year (Gayot *et al.*, 2004; Ho Tong Minh *et al.*, 2016; Richard-Hansen *et al.*, 2015). It experiences a dry season from August to November (driest months are September and October), and a rainy season between December and July, with a possible small dry season in February or March.

Camera trapping protocol and data collection

A total of 34 (21 HC600 Hyperfire, 8 Hyperfire2, and 5 XR6 Ultrafire) camera traps equipped with infrared motion sensors were installed within the crowns of 11 trees (mostly *Virola kwatae* and *Virola michelii* and only one in a fruiting Sapotaceae tree) ranging from 30 to 40 meters high, and used by

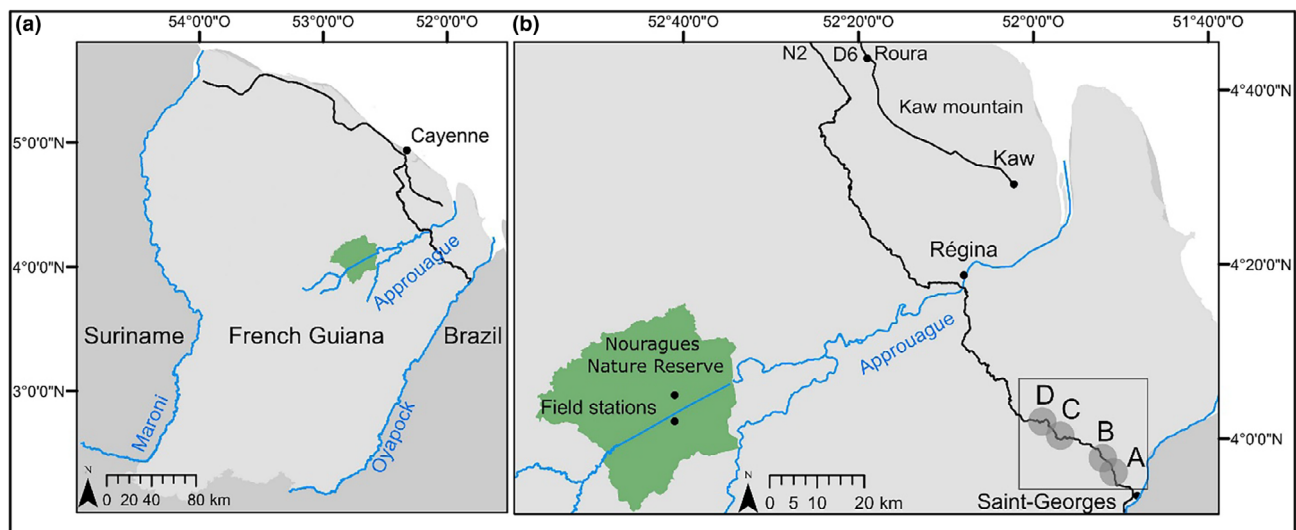


Figure 1 Map of study area showing camera trap clusters (A, B, C, and D) and their respective locations (Adapted from Coutant *et al.*, 2022).

frugivorous mammals. Camera traps were installed for an average duration of 50 days (range = 12–93 days) between the years 2019 and 2022. In each tree, camera traps were set on the trunk, and within the main branches for maximum coverage, with each trap configured to take five photographs when movement was detected (see detailed protocol description in Coutant *et al.*, 2022 and Séguigne *et al.*, 2022). Camera traps were also configured to continuously take pictures for up to 120 min when animals remained mobile within its focal range. However, data presented here only included pictures captured by a total of 27 camera traps for trees where kinkajous were observed. Following home-range information from previous studies (Julien-Laferriere, 1993; Kays & Gittleman, 1995), camera traps from which data were obtained were grouped into four separate clusters on the basis that each cluster may have captured a single individual within a given home range. We grouped camera traps such that each cluster was separated by a distance of at least 3.5 km and comprised at least one camera trap (range = 1–20 camera traps per cluster on 1 to 10 fruiting trees) located within 250 m radius of each other (clusters A, B, C and D; Fig. 1b).

We considered a group of at least three consecutive photos as a single observational event (periods of activities and behavioral gestures). Since at least 5 seconds interval was the required time without activity for a camera trap to stop taking pictures, collective groups of consecutive photos separated by five or more seconds were considered as separate observational events. Within each observational event, we described the different activities (i.e., engagement in a particular task), times of each activity, and their corresponding positional behaviors using photos that captured complete or almost complete bodies of the focal individuals. For observational events where multiple activities and positional behaviors were observed, we recorded each as a separate activity and/or positional behavior within the same observational event. Activities were categorized as scanning, traveling, climbing, bridging, leaping,

dropping, descending, foraging, feeding, grooming, or resting (Table 1). Positional behaviors were mostly classified using behavioral descriptions adopted from Hunt *et al.* (1996) (Table 2). We further grouped times of activities as either active or inactive periods. Active periods included times when kinkajous were more alert, mobile, and engaged in different activities (e.g., traveling, climbing, bridging, leaping, dropping, descending, foraging, and feeding) while inactive periods were times when kinkajous were comparatively less active (e.g. resting and grooming). Scanning activities were excluded from this grouping since it was observed during both active and inactive periods, hence, being less indicative of either category.

Data analysis

All data analyses and visualizations were performed in RStudio Version 4.3.2 (2023-10-31) using the “dplyr” (Wickham *et al.*, 2023), “ggplot2” (Wickham, 2016), “tidyverse” (Wickham *et al.*, 2019), “lubridate” (Grolemund & Wickham, 2011), “cowplot” (Wilke, 2020), “patchwork” (Pedersen, 2023), “reshape” (Wickham, 2007), “gridExtra” (Auguie, 2017), and “density” (Deng & Wickham, 2011) packages. Gantt charts were used to show the timing of different activities during the entire duration of active and inactive periods. Data were analyzed using a descriptive statistical approach to quantify the activities by estimating the frequency of an activity as a percentage of the number of observational events in which said activity was observed divided by the total number of observational events. Positional behaviors displayed during each activity were computed as the number of observational events where specific locomotor or postural behaviors were observed divided by the total number of observational events within which the activity was observed. Additionally, behaviors and activities were analyzed separately in instances where observational events captured multiple positional behaviors and activities. Consequently, this yielded percentages that may exceed

Table 1 Ethogram established for *Potos flavus*

Activity state	Definitions
Traveling	General movement of individual from one point to another on a continuous horizontal or sub-horizontal substrate
Climbing	An upward progression on vertical substrates using various limb combinations
Descending	A downward progression on a vertical substrate using various limb combinations
Leaping	A gap-crossing movement in which hind limbs are mainly used as propulsion and there is an extended period of free flight
Dropping	Movement from a higher stratum substrate to a lower stratum substrate where take off is initiated by falling after releasing the support
Bridging	Movement across two discontinuous substrates where hind limbs or tail remain in contact with previous substrate while it reaches for another substrate across the gap
Foraging	Searching behaviors directed toward a potential food source within foliage and/or small branches of trees
Feeding	Processing, handling, and consumption behaviors when holding food
Scanning	Visual inspection of surrounding area while momentarily remaining in a single position
Grooming	When individual is licking or scratching itself or another individual
Resting	When individual is immobile with its ventral body surface on substrate

100% when the total activities and positional behaviors are summed. For instance, if there were four instances of traveling and two instances of resting activities observed across five observational events with one observational event having both traveling and resting activities, this would result in 80% and 40% of the observational events including traveling and resting activities, respectively, hence making a combined total of 120%.

Results

Overall, we analyzed a total of 2223 photographs making up 418 observational events (206 locomotor events and 307 postural events) from at least four (but possibly more) individuals. Kinkajous showed a strict nocturnal activity pattern starting from around 19:00 h to 05:57 h with a gradual increase in frequency of activities until the peak active period between 01:00 h and 02:00 h, after which there was a gradual decrease (Fig. 3). Results further showed a total occurrence of 12 activities (nine during active periods, two during inactive periods, and one during both periods) and 34 positional behaviors (17 locomotor and postural behaviors each). Scanning and traveling were the most frequently observed activities (48.33% and 47.13%, respectively; Fig. 2), occurring throughout the entire nocturnal period. Conversely, feeding was the least observed activity (0.48%) and was only recorded about 2 h before sunrise, during which individuals assumed a squatting posture (Fig. 3 and Table 3).

Active periods were primarily characterized by traveling (92.23%) and climbing (45.36%) behaviors. Kinkajous used quadrupedal walk (95.43%) as their main locomotor behavior when traveling (Fig 4). However, when crossing gaps between two substrates (i.e., branches), they either bridged (42.22%), leaped (33.33%), or dropped (26.67%) depending on the height and horizontal distance between the two substrates. Upward vertical bridging (57.89%) was a common bridging behavior used to cross gaps from low level to higher level substrates while tail suspend drop made up 58.33% of all dropping

behaviors used to cross gaps from higher to lower substrates. Nevertheless, when crossing gaps between substrates of about the same level, kinkajous preferred to leap or bridge, specifically engaging in a pronograde leap (100%) or cautious pronograde bridge (36.1%). They also assumed either a quadrupedal stance, a bimanual forelimb crouch, sitting, or full crouching postures at a respective 45.54%, 22.28%, 21.29%, and 19.31% when scanning or exploring their immediate environment (Table 3). During inactive periods, we observed individuals mainly engaging in 77.32% of grooming activities as opposed to 27.84% of resting (Table 3). Ninety-six percent of the grooming activities involved self-grooming behaviors (65% and 40.28% licking and scratching behaviors, respectively) while assuming a sitting posture (90.67%), but resting consisted predominantly of catlike body curl postures (92.59%; Table 3) (Fig 5).

Discussion

This study highlights the broad array of positional behaviors and activity patterns displayed by kinkajous and the use of camera traps as a relevant and less intrusive methodological approach in assessing such behaviors in arboreal nocturnal animals in their natural habitats. In natural environments, movement is a major component of an animal's daily activity, allowing it to exploit available food resources, patrol territories, and search for potential mates (Resende *et al.*, 2014). Similar to reports from Julien-Laferriere (1993), we found that kinkajous spent a significant amount of time traveling (specifically quadrupedal walking) through their environment. This may be due to the fact that kinkajous within the study area have been shown to be predominantly frugivorous, feeding on a wide variety of fruits and nectar (Coutant *et al.*, 2022; Julien-Laferriere, 1993; Séguigne *et al.*, 2022). Compared to leaves, fruits may be patchily distributed in the environment and therefore, frugivorous animals such as kinkajous may have to invest more time and effort traveling in search of them. Alternatively, the high frequency of kinkajou movement may

Table 2 Ethogram of positional behaviors of *Potos flavus*

Positional behaviors	Definitions
Locomotor behaviors	
Quadrupedal walk	Slow pronograde progression on a horizontal or sub-horizontal substrate with body upright and all four limbs bear body weight
Crouched quadrupedal walk	Slow pronograde progression similar to that of the quadrupedal walk where the body is lowered closer to the substrate than usual
Inverted quadrupedal walk	Slow pronograde progression on ventral side of a horizontal substrate with all four limbs in contact with the substrate and sometimes aided by the tail
Cling walk	Slow pronograde progression where a single or both pair of limbs tightly hold the substrate during at least one point of the gait sequence
Quadrupedal run	Rapid pronograde progression on top of a horizontal or sub-horizontal substrate where all four limbs bear body weight
Pronograde leap	Gap crossing leaping movement initiated from either a postural or a locomotor position where the torso is primarily pronograde at take-off
Flexed elbow vertical climb	Upward ascent on vertical substrates where the hind limb together with its contralateral forelimb provide propulsion to elevate the body
Ladder climb	Upward progression on a series of horizontal supports following a diagonal sequence movement of limbs. Similar to a person climbing a ladder
Pulse climb	A vertically ascent where forelimbs grasp a higher support, the hind limbs are gathered beneath the body by flexion of the knee, hip, and spine and the extension of hind limbs and back pushes the body upwards
Bimanual pull up	Upward progression where horizontal support is grasped by both forelimbs and the body is hoisted up by retracting the forelimbs
Head-first descent	Downward descent on a vertical substrate with quadrupedal movement while the head faces down
Cautious pronograde bridge	A pronograde gap crossing movement where the forelimb first grasps the distant support and the hind limbs release their grip from the original substrate to move onto the new support
Supinograde bridge	Gap crossing movement from an upper substrate to a lower substrate from a suspensory posture where hands are used to grasp lower substrate before crossing
Upward vertical bridge	Upward gap crossing movement where forelimbs grasp higher substrate with hind limbs still on lower substrate followed by a lunge upwards
Quadrupedal drop	A dropping movement from higher substrate to lower substrate where prior posture is indistinguishable from quadrupedal or tripodal stance
Tail-suspend drop	A dropping movement from higher substrate to lower substrate where animal assumes a tail suspend posture just before drop
Tail-hind limb suspend drop	A dropping movement from higher substrate to lower substrate where animal assumes a tail hind limb suspend posture just before drop
Postural behaviors	
Tail-suspend	Suspensory posture with tail alone used to hang below a substrate
Tail-hind limb suspension	Suspensory posture with substantial support from a combination of the extended hind limb and the tail used to hang below a substrate
Trunk vertical suspension	An orthograde suspensory posture with head superior and various combinations of all four limbs attached to substrates in different ways
Hind limb suspension	Suspensory posture where the body hangs below substrate and is only supported by the extended hind limbs
Quadrupedal stance	A posture in which four limbs are standing on horizontal or sub-horizontal substrate
Bipedal stance	Standing on hind limbs where torso is usually held at an orthograde position but may sometimes be held in a pronograde position
Prone	A ventral lying position on horizontal substrate with limbs usually tucked in
Sit	A stationary posture in which the ischia is used to support the body with varying limb and tail placements
Squat	A posture in which both hip and knee are strongly flexed, and the body weight is borne solely by the feet
Bimanual cling	A posture on substrate where both forelimbs and hind limbs grasp substrate with a power grip and body pronograde to substrate
Hind limb cling	A posture on substrate where the hind limb grasps substrate with a power grip and body pronograde to substrate
Tripodal posture	Combination of tail suspend and bipedal standing where animal has both hind limbs pressing on a substrate and tail is anchored to a different substrate
Full crouch	A position where both elbows and hind limbs are flexed and the whole torso body is brought close to the substrate
Bimanual forelimb crouch	A posture where both forelimbs are flexed and the upper torso is brought close to the substrate
Unimanual forelimb crouch	A posture where a single forelimb is flexed, and the upper torso is brought close to the substrate while the other forelimb is used in other activities
Body curl	A ball-like lying posture with the head bent toward the feet and tail is tucked in
Sideways lie	A posture where the individual lies on one of its lateral sides with belly half exposed and legs out

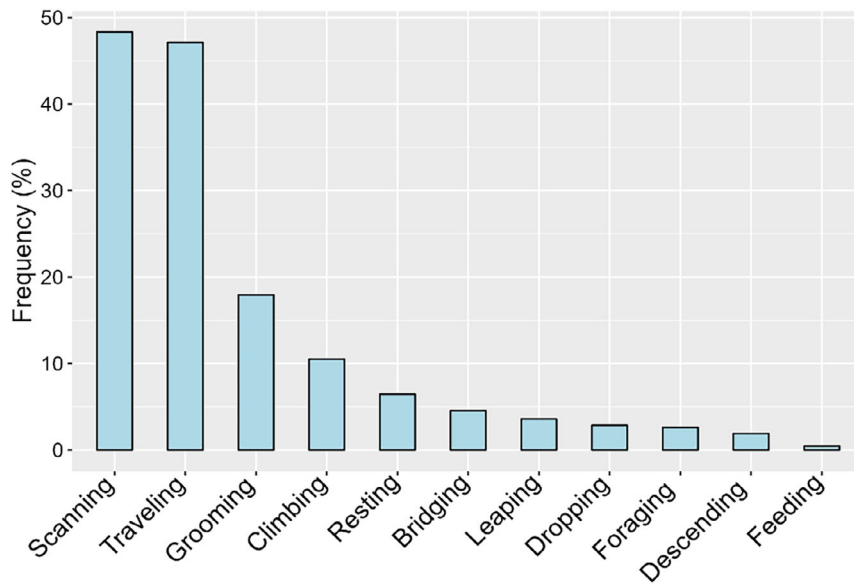


Figure 2 Frequencies of occurrence of various nocturnal activities of kinkajous.

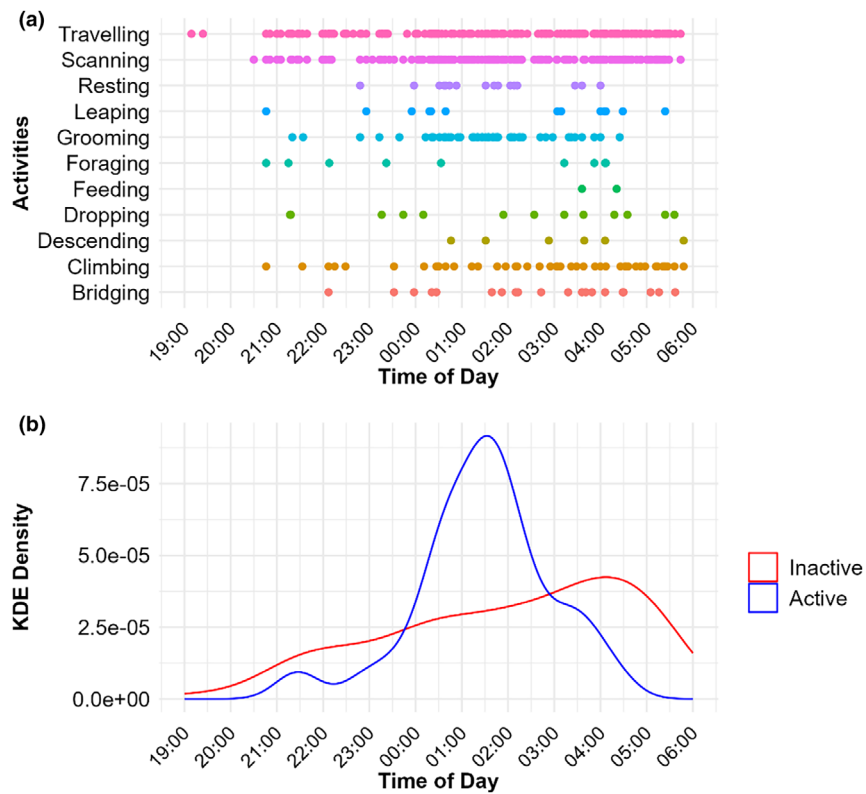


Figure 3 Activity-time patterns (a) and trends of active and inactive periods (b). Active periods are characterized by kinkajous being more alert, mobile, and engaged in various activities while inactive periods are characterized by kinkajous being comparatively less active and/or rest. KDE densities represent the distribution expressed as the probability density per unit of time (1/h) of active and inactive periods within a given time interval.

Table 3 Frequencies of occurrence of positional behaviors associated with each activity (*N* = Number of observational events)

Periods	Activity	Obs. (<i>N</i>)	Positional behaviors	Obs. (%)
Active periods	Traveling	197	Quadrupedal walk	95.43
			Crouched quadrupedal walk	4.06
			Quadrupedal run	1.02
			Inverted quadrupedal walk	1.02
			Cling walk	1.02
	Foraging	11	Tail suspend	9.09
			Tail-hind limb suspend	9.09
			Tripodal posture	27.27
			Bipedal stance	27.27
			Hind limb suspend	9.09
			Hind limb cling	9.09
			Unimanual forelimb crouch	9.09
			Flexed elbow vertical climb	45.45
	Climbing	44	Bimanual pull up	27.27
			Ladder climb	25
			Pulse climb	11.36
	Dropping	12	Quadrupedal drop	25
			Tail-suspend drop	58.33
			Tail-hind limb suspend drop	16.67
	Bridging	19	Cautious pronograde bridge	31.58
Supinograde bridge			10.53	
Upward vertical bridge			57.89	
Leaping	15	Pronograde leap	100	
		Head first descent	100	
		Squat	100	
Inactive periods	Grooming	75	Sitting	90.67
			Squatting	4
			Body curl	2.67
			Quadrupedal stance	1.33
			Bipedal stance	1.33
			Sideways lie	1.33
			Body curl	92.59
			Sideway lie	7.41
			Prone	14.81
			Quadrupedal stance	45.54
	Resting	27	Bipedal stance	4.46
			Sit	21.29
			Prone	2.48
			Squat	6.44
			Bimanual cling	0.5
			Full crouch	19.31
			Trunk vertical suspend	1.49
	Scanning	202	Bimanual forelimb crouch	22.28
			Hind limb cling	1.49
			Tail hind limb suspend	0.5

be an activity directed toward patrolling, marking, and defense of territories. Indeed, kinkajous have been observed to exhibit territorial behaviors by marking areas encircling suitable food resources and engaging in aggressive defensive behaviors toward male conspecifics from other groups (Kays & Gittleman, 1995).

One of the challenges faced by highly arboreal species when moving within their environment is the crossing of gaps between supports (Druelle *et al.*, 2020). McClearn (1992) observed that kinkajous crossed gaps mainly by bridging

between the gaps. However, there has been some conflicting data on whether kinkajous slowly and cautiously bridge gaps (Enders & Enders, 1935) or leap across them (Emmons, 1990). According to Bezanson (2006), factors such as substrate (*i.e.*, branch) use, and the length of the body and limbs are likely to affect positional behaviors used for gap crossing in arboreal species. In that respect, it is possible that kinkajous may employ either leaping or bridging depending on the size of substrates involved as well as the width of the gap between said substrates. Our data support these claims. Interestingly, we

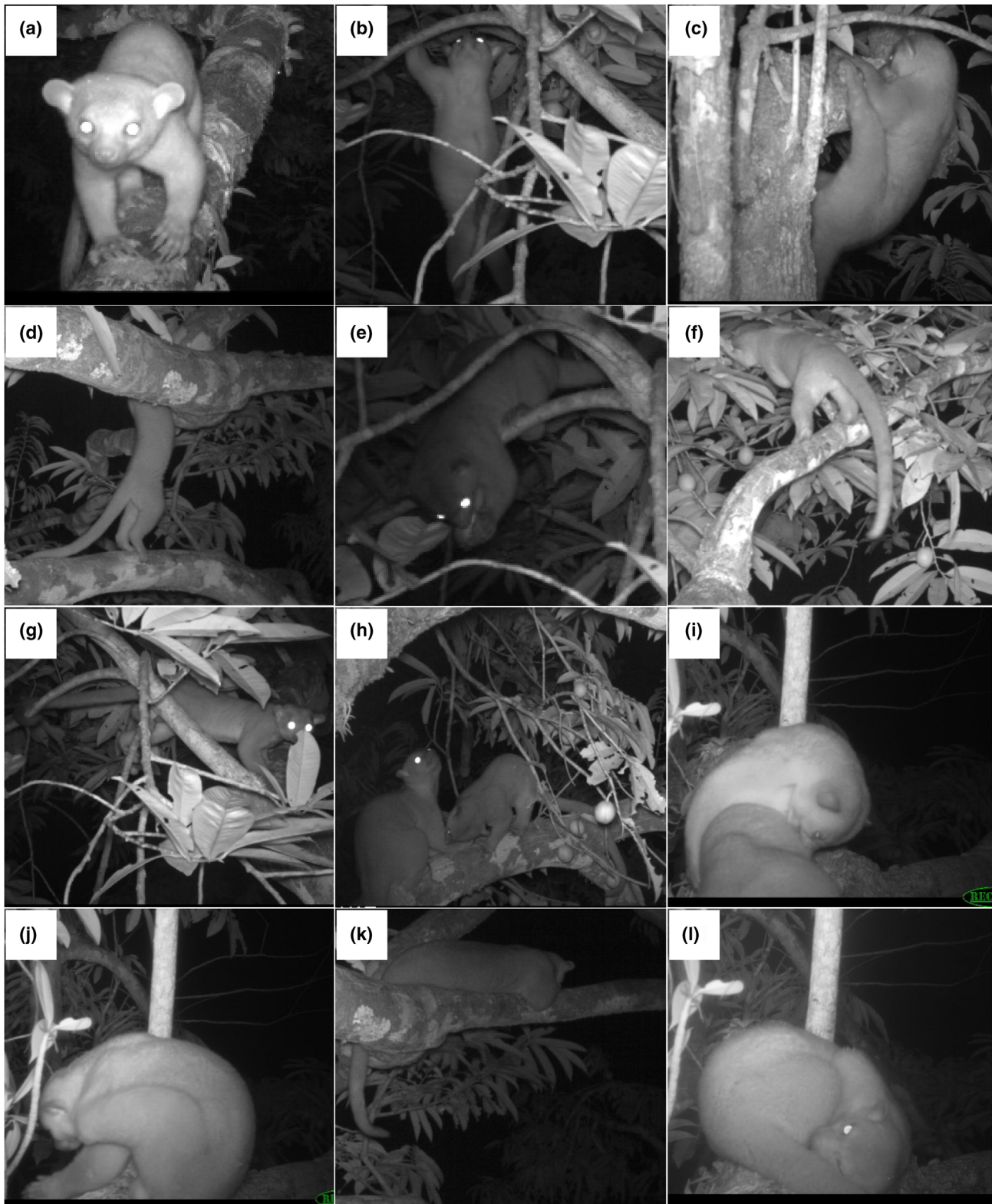


Figure 4 Some positional behaviors observed during active (a: *Quadrupedal walk*, b: *Ladder climb*, c: *Pulse climb*, d: *Upward vertical bridge*, e: *Squat during feeding*, f: *Bipedal stance during foraging*, g: *Cautious pronograde bridge*) and inactive periods (h: *Allgrooming*, i: *Autogrooming by licking*, j: *Autogrooming by scratching*, k: *Prone*, l: *Body curl*).

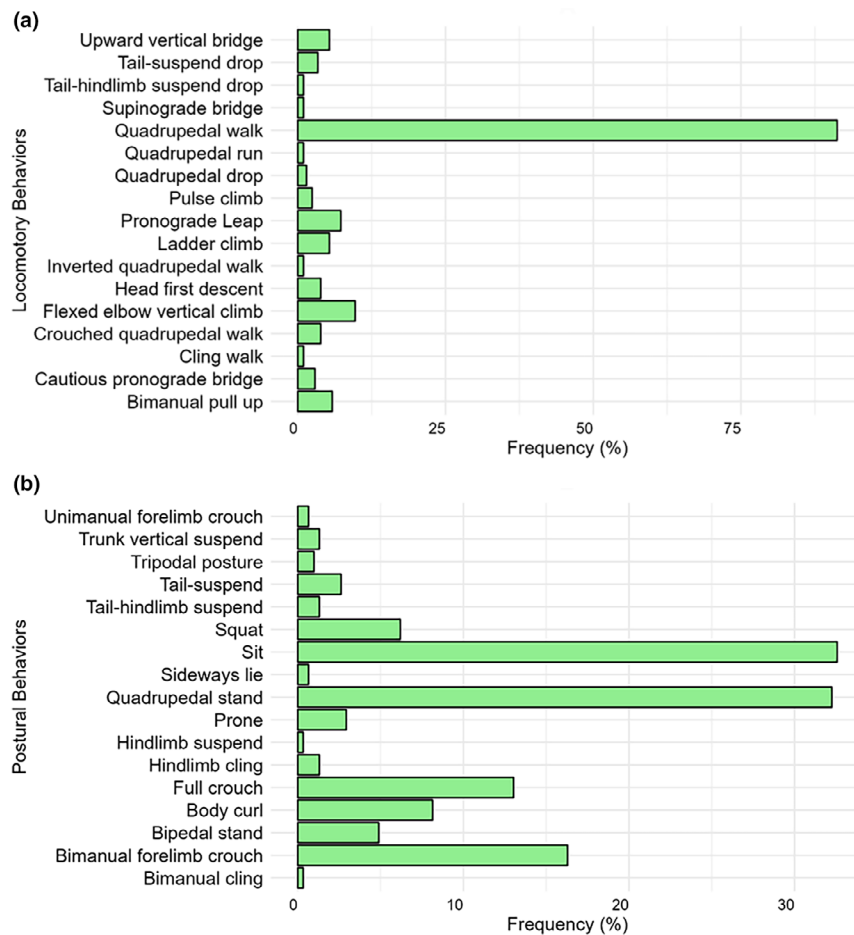


Figure 5 Overall frequencies of occurrence of observed locomotor (a) and postural behaviors (b) displayed by kinkajous.

noticed that leaping was used between relatively medium to large substrates with gap widths typically larger than their body length, while slow bridging was employed between small and medium to large substrates with smaller gap widths. Although these are preliminary observations that were not systematically analyzed, quantified, and presented in this study (details presented in a follow up publication), they however, indicate a potential substrate size effect on arboreal behaviors as mentioned by Séguigne *et al.* (2022). Thus, we recommend that subsequent studies may benefit from exploring substrate size and stability as factors likely affecting positional behaviors, not only in kinkajous, but also other arboreal species.

We observed grooming to be a major behavior during inactive periods. Grooming is an important adaptation in mammals to care for their body surfaces by keeping the integument clean from parasites (Bush & Clayton, 2023). This activity may be either performed by the same individual (self-grooming or autogrooming) or by other conspecific individuals (allogrooming). As such, grooming behaviors do not only serve hygienic purposes, but also play an important role in the establishment and maintenance of social bonds (Molesti & Majolo, 2013). Studies have reported the engagement of kinkajous in

allogrooming behaviors especially when in social groups (Kays & Gittleman, 2001). However, in this study, we recorded a rather higher frequency of self-grooming behaviors. Kays and Gittleman (2001), found that allogrooming was largely directed toward the upper parts of the body, including the head, ears, and neck regions. In contrast to this, all self-grooming behaviors observed in this study were directed toward the lower torso, including the hind limbs, tail, genitals, and abdominal regions. This would suggest that kinkajous may engage in allogrooming not only for social bonding purposes as reported by Kays and Gittleman (2001), but also to reach parts of the body that may otherwise be difficult to reach during self-grooming.

We further noticed that grooming behaviors were mostly before or after resting. McClearn (1992) observed that kinkajous either lie sideways (which she called right side up) or upside-down when resting. Although our data were consistent with lying sideways, records of this posture were scant. Rather, kinkajous were mainly observed to assume a catlike body curl posture when resting. According to Lopes and Bicca-Marques (2017), animals may use body postures to change their surface-to-volume ratio for the purpose of regulating heat dissipation. Consequently, heat exchange between

animals and their environment is greatly reduced when they assume postures that keep their limbs close to the torso. Thus, for kinkajous, the major use of body curl and even proning postures when resting may act as a thermoregulatory adaptive behavior to conserve energy. To the best of our knowledge, this is the first observation of body curl together with proning postures during resting in kinkajous. On the other hand, the use of these postures during resting activities may be a function of substrate size such that kinkajous potentially exhibit the best and most efficient resting postures based on branch size and stability. However, since substrate size was not measured within the scope of this study, we are unable to explore this further.

Interestingly, kinkajous displayed a wide array of food acquisition postural behaviors when foraging. Although most of these postures were observed on very few occasions, it nonetheless highlights the capabilities of this species to exploit food resources on different parts of the tree canopy. Similar postures and behaviors were recorded by McClearn (1992), who also reported the use of sitting and hanging postures as feeding behaviors in kinkajous. She further argued that these postures free the forelimbs, allowing for efficient food manipulation. We did record the use of squatting posture during which the focal individual leaned forward and downwards while manipulating food with its free forearms. This observation adds to the existing knowledge of the various feeding postures of kinkajous and in part, supports McClearn's (1992) observations.

Previous studies of the activity pattern of kinkajous using radio tags showed that kinkajous were strictly nocturnal, with activities commencing shortly after sunset and lasting for about 8 h in females and 10 h in males (Julien-Laferriere, 1993). Findings from the current study indicated that kinkajous exit their day dens a few minutes after sunset with activities lasting at least 10 h, in accordance with the observations of Julien-Laferriere (1993), and complementary to a previous study by Séguigne *et al.* (2022). Other studies have also confirmed the strict nocturnality of kinkajous both in captivity (Kavanau & Ramos, 1972) and in the wild (Kays & Gittleman, 2001). Moreover, Kays and Gittleman (2001) also observed that some adult males become active few minutes before sunset during reproductive periods. Séguigne *et al.* (2022) argued that the strict nocturnality of kinkajous may be a behavioral adaptation to avoid spatio-temporal niche competition with other diurnal frugivores such as tufted capuchins (*Sapajus apella*, Linnaeus 1758) and Guyana red howlers (*Alouatta macconnelli*, Linnaeus, 1766) with which they share a large part of their diet and home range. However, due to little information on feeding periods recorded in this study as a result of limited sampling, we are unable to effectively disentangle feeding time allocation of kinkajous. This could be attributed to the behavior of kinkajous, as they primarily forage on both large and small branches situated in the background (Forget *et al.*, unpublished field observation). As a result, they are rarely observed eating directly in front of the cameras. Moreover, since photos taken by camera traps may also have the potential of taking a small fragment of an activity due to its limited range of coverage, it is possible that some activities

and behaviors observed here may be a fraction of unobserved ones. This raises the likelihood of overlooking additional activities and positional behaviors exhibited in ecologically significant contexts and areas that may have been missed in this study. Additionally, given that activity patterns may also be subjected to seasonal changes (Suzuki & Ando, 2017), and that the current study primarily focused on the general activity patterns of kinkajous, it remains possible that there exist seasonal variation in the activity patterns of kinkajous that may not have been highlighted. In these regards, we recommend that camera trap sampling efforts prioritize camera trap stations at key ecological areas such as feeding sites and individual dens (along with its surrounding areas) to capture a broader range of positional behaviors and activities while simultaneously incorporating the effect of seasonal changes on the dynamics of activity patterns and positional behaviors of kinkajous. One other noteworthy shortcoming of the current study has to do with the number of individuals captured by camera traps. Although individuals were isolated based on a group of camera traps stationed in and out of potential home ranges, this does not exclude the fact that multiple individuals may have been moving around in the same tree since kinkajous often move in ones or twos (Julien-Laferriere, 1993). As such, it is possible that there exist potential individual differences that may not have been highlighted here.

Conclusion

In summary, our study showed that kinkajous display a wide combination of primate-like and catlike positional behaviors, consequently highlighting how kinkajous interact with their immediate environment. Moreover, this study showed that kinkajous not only spend most of their nocturnal active periods traveling through their home range, but also spend a significant amount of time grooming and resting during inactive periods. It also provides relevant information for understanding the basic ecology and eco-evolutionary dynamics of the species in comparison to other mammals such as felids and primates that may display similar positional behaviors. The study further provides a baseline documentation of positional behaviors useful for training Artificial Intelligence (AI) analysis of camera traps or Accelerometer data obtained from data collars through which other positional behaviors can be studied.

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Conflict of interest

The authors declare no competing interests.

Additional information

All pictures used in this project are available on the database upon request, agreement, and authorization.

Author contributions

JBM, AH, and AGN conceived the idea; PMF and EG engaged in fieldwork, climbed and installed camera traps in selected *Virola spp.* and *Manikara spp.* trees; PMF entered pictures into the agouti.eu platform, and labeled them. PMF is also PI of the Agouti.eu database; JBM retrieved data from the Agouti.eu database platform, cleaned and manipulated, analyzed, and visualized data; JBM, AH, AGN, and BYO contributed to contextualization and interpretation of results; JBM led the writing of the paper with contributions from all other authors. All authors contributed critically to the drafts and gave final approval for publication.

References

- Astiazarán Azcarraga, A., Gallina Tessaro, S., Delfin-Alfonso, C. A., Astiazarán Azcarraga, A., Gallina Tessaro, S., & Delfin-Alfonso, C. A. (2020). Activity patterns of arboreal mammals in a tropical rain forest in México. *Therya*, *11*(2), 225–231. <https://doi.org/10.12933/therya-20-779>
- Auguie, B. (2017). *GridExtra: Miscellaneous functions for "grid" graphics*. R package version 2.3. <https://CRAN.R-project.org/package=gridExtra>
- Bezanson, M. (2017). Primate positional behavior development and evolution. *Annual Review of Anthropology*, *46*(1), 279–298. <https://doi.org/10.1146/annurev-anthro-102116-041503>
- Bezanson, M., & Morbeck, M. E. (2013). Future adults or old children? Integrating life history frameworks for understanding primate positional patterns. In K. B. H. Clancy, K. Hinde, & J. N. Rutherford (Eds.), *Building babies: Primate development in proximate and ultimate perspective* (pp. 435–458). Springer. https://doi.org/10.1007/978-1-4614-4060-4_19
- Bezanson, M. F. (2006). Leap, bridge, or ride? Ontogenetic influences on positional behavior in Cebus and Alouatta. In A. Estrada, P. A. Garber, M. S. M. Pavelka, & L. Luecke (Eds.), *New perspectives in the study of Mesoamerican primates: Distribution, ecology, behavior, and conservation* (pp. 333–348). Springer. https://doi.org/10.1007/0-387-25872-8_16
- Bicca-Marques, J. C., & Calegario-Marques, C. (2008). Feeding postures in the black howler monkey, *Alouatta caraya*. *Folia Primatologica*, *60*(3), 169–172. <https://doi.org/10.1159/000156686>
- Blake, J., Mosquera, D., Loisele, B., Swing, K., Guerra, J., & Romo, D. (2012). Temporal activity patterns of terrestrial mammals in lowland rainforest of eastern Ecuador. *Ecotropica*, *137*, 137–146.
- Bush, S. E., & Clayton, D. H. (2023). Grooming time predicts survival: American kestrels, *Falco sparverius*, on a Subtropical Island. *The American Naturalist*, *201*(4), 603–609. <https://doi.org/10.1086/723412>
- Chatani, K. (2003). Positional behavior of free-ranging Japanese macaques (*Macaca fuscata*). *Primates*, *44*(1), 13–23. <https://doi.org/10.1007/s10329-002-0002-z>
- Coutant, O., Boissier, O., Ducretet, M., Albert-Daviaud, A., Bouiges, A., Dracxler, C. M., Feer, F., Mendoza, I., Guilbert, E., & Forget, P.-M. (2022). Roads disrupt Frugivory and seed removal in tropical animal-dispersed plants in French Guiana. *Frontiers in Ecology and Evolution*, *10*, 805376. <https://doi.org/10.3389/fevo.2022.805376>
- Daloz, M. F., Loretto, D., Papi, B., Cobra, P., & Vieira, M. V. (2012). Positional behaviour and tail use by the bare-tailed woolly opossum *Caluromys philander* (Didelphimorphia, Didelphidae). *Mammalian Biology*, *77*(5), 307–313. <https://doi.org/10.1016/j.mambio.2012.03.001>
- Deng, H., & Wickham, H. (2011). *Density estimation in R*. Electronic Publication.
- Druelle, F., Aerts, P., Ngawolo, J. C. B., & Narat, V. (2020). Impressive arboreal gap-crossing behaviors in wild bonobos, pan paniscus. *International Journal of Primatology*, *41*(1), 129–140. <https://doi.org/10.1007/s10764-020-00140-z>
- Emmons, L. H. (1990). *Neotropical rainforest mammals: A field guide*. <https://cir.nii.ac.jp/crid/1130000796403878272>
- Enders, R. K., & Enders, R. K. (1935). Mammalian life histories from Barro Colorado Island, Panama. *Bulletin of the Museum of Comparative Zoology at Harvard College*, *78*, 385–502.
- Gayot, M., Henry, O., Dubost, G., & Sabatier, D. (2004). Comparative diet of the two forest cervids of the genus *Mazama* in French Guiana. *Journal of Tropical Ecology*, *20*(1), 31–43. <https://doi.org/10.1017/S0266467404006157>
- Gracanian, A., & Mikac, K. M. (2022). Camera traps reveal overlap and seasonal variation in the diel activity of arboreal and semi-arboreal mammals. *Mammalian Biology*, *102*(2), 341–355. <https://doi.org/10.1007/s42991-021-00218-y>
- Grolemund, G., & Wickham, H. (2011). Dates and Times Made Easy with lubridate. *Journal of Statistical Software*, *40*, 1–25. <https://doi.org/10.18637/jss.v040.i03>
- Guitet, S., Pélissier, R., Brunaux, O., Jaouen, G., & Sabatier, D. (2015). Geomorphological landscape features explain floristic patterns in French Guiana rainforest. *Biodiversity and Conservation*, *24*(5), 1215–1237. <https://doi.org/10.1007/s10531-014-0854-8>
- Halle, S., & Stenseth, N. C. (2000). *Activity patterns in small mammals: An ecological approach; with 11 tables*. Springer Science and Business Media.
- Ho Tong Minh, D., Le Toan, T., Rocca, F., Tebaldini, S., Villard, L., Réjou-Méchain, M., Phillips, O. L., Feldpausch, T. R., Dubois-Fernandez, P., Scipal, K., & Chave, J. (2016).

- SAR tomography for the retrieval of forest biomass and height: Cross-validation at two tropical forest sites in French Guiana. *Remote Sensing of Environment*, **175**, 138–147. <https://doi.org/10.1016/j.rse.2015.12.037>
- Hunt, K. D., Cant, J. G. H., Gebo, D. L., Rose, M. D., Walker, S. E., & Youlatos, D. (1996). Standardized descriptions of primate locomotor and postural modes. *Primates*, **37**(4), 363–387. <https://doi.org/10.1007/BF02381373>
- Ikeda, T., Uchida, K., Matsuura, Y., Takahashi, H., Yoshida, T., Kaji, K., & Koizumi, I. (2016). Seasonal and diel activity patterns of eight sympatric mammals in northern Japan revealed by an intensive camera-trap survey. *PLoS One*, **11**(10), e0163602. <https://doi.org/10.1371/journal.pone.0163602>
- Julien-Laferrrière, D. (1993). Radio-tracking observations on ranging and foraging patterns by kinkajous (*Potos flavus*) in French Guiana. *Journal of Tropical Ecology*, **9**(1), 19–32. <https://doi.org/10.1017/S0266467400006908>
- Julien-Laferrrière, D. (2001). Frugivory and seed dispersal by kinkajous. In F. Bongers, P. Charles-Dominique, P.-M. Forget, & M. Théry (Eds.), *Nouragues: Dynamics and plant-animal interactions in a Neotropical rainforest* (pp. 217–226). Springer. https://doi.org/10.1007/978-94-015-9821-7_20
- Kavanau, J. L., & Ramos, J. (1972). Twilights and onset and cessation of carnivore activity. *The Journal of Wildlife Management*, **36**(2), 653–657. <https://doi.org/10.2307/3799104>
- Kays, R. W. (1999). Food preferences of kinkajous (*Potos flavus*): A frugivorous carnivore. *Journal of Mammalogy*, **80**(2), 589–599. <https://doi.org/10.2307/1383303>
- Kays, R. W., & Gittleman, J. L. (1995). Home range size and social behavior of kinkajous (*Potos flavus*) in the Republic of Panama. *Biotropica*, **27**(4), 530–534. <https://doi.org/10.2307/2388969>
- Kays, R. W., & Gittleman, J. L. (2001). The social organization of the kinkajou *Potos flavus* (Procyonidae). *Journal of Zoology*, **253**(4), 491–504. <https://doi.org/10.1017/S0952836901000450>
- Kays, R. W., Gittleman, J. L., & Wayne, R. K. (2000). Microsatellite analysis of kinkajou social organization. *Molecular Ecology*, **9**(6), 743–751. <https://doi.org/10.1046/j.1365-294x.2000.00921.x>
- Li, P.-H., Li, W.-B., Li, B.-W., Li, Y.-D., Wang, X., & Li, J.-H. (2022). Positional behavior and substrate use in wild Tibetan macaques. *Animals*, **12**(6), 6. <https://doi.org/10.3390/ani12060767>
- Lopes, K. G. D., & Bicca-Marques, J. C. (2017). Ambient temperature and humidity modulate the behavioural thermoregulation of a small arboreal mammal (*Callicebus bernhardi*). *Journal of Thermal Biology*, **69**, 104–109. <https://doi.org/10.1016/j.jtherbio.2017.06.010>
- McClearn, D. (1992). Locomotion, posture, and feeding behavior of kinkajous, coatis, and raccoons. *Journal of Mammalogy*, **73**(2), 245–261. <https://doi.org/10.2307/1382055>
- Molesti, S., & Majolo, B. (2013). Grooming increases self-directed behaviour in wild barbary macaques, *Macaca sylvanus*. *Animal Behaviour*, **86**(1), 169–175. <https://doi.org/10.1016/j.anbehav.2013.05.008>
- Monterroso, P., Alves, P. C., & Ferreras, P. (2013). Catch me if you can: Diel activity patterns of mammalian prey and predators. *Ethology*, **119**(12), 1044–1056. <https://doi.org/10.1111/eth.12156>
- Ota, A., Takagi, E., Yasuda, M., Hashim, M., Hosaka, T., & Numata, S. (2019). Effects of nonlethal tourist activity on the diel activity patterns of mammals in a National Park in peninsular Malaysia. *Global Ecology and Conservation*, **20**, e00772. <https://doi.org/10.1016/j.gecco.2019.e00772>
- Pedersen, T. (2023). *Patchwork: The composer of plots*. R package version 1.1.3. <https://CRAN.R-project.org/package=patchwork>
- Ramírez-Mejía, A., & Sánchez, F. (2016). Activity patterns and habitat use of mammals in an Andean forest and a eucalyptus reforestation in Colombia. *Hystrix, the Italian Journal of Mammalogy*, **27**(2), 104–110. <https://doi.org/10.4404/hystrix-27.2-11319>
- Resende, L. d. S., Neto, G. L. e., Carvalho, P. G. D., Landau-Remy, G., Ramos-Júnior, V. d. A., Andriolo, A., & Genaro, G. (2014). Time budget and activity patterns of *Oncilla* cats (*Leopardus tigrinus*) in captivity. *Journal of Applied Animal Welfare Science*, **17**(1), 73–81. <https://doi.org/10.1080/10888705.2014.856253>
- Richard-Hansen, C., Jaouen, G., Denis, T., Brunaux, O., Marcon, E., & Guitet, S. (2015). Landscape patterns influence communities of medium- to large-bodied vertebrates in undisturbed terra firme forests of French Guiana. *Journal of Tropical Ecology*, **31**(5), 423–436. <https://doi.org/10.1017/S0266467415000255>
- Séguigne, M., Coutant, O., Bouton, B., Picart, L., Guilbert, É., & Forget, P. M. (2022). Arboreal camera trap reveals the frequent occurrence of a frugivore-carnivore in Neotropical nutmeg trees. *Scientific Reports*, **12**(1), 1. <https://doi.org/10.1038/s41598-022-11568-z>
- Stafford, B. J., Thorington, R. W., Jr., & Kawamichi, T. (2003). Positional behavior of Japanese Giant flying squirrels (*Petaurista leucogenys*). *Journal of Mammalogy*, **84**(1), 263–271. [https://doi.org/10.1644/1545-1542\(2003\)084<0263:PBOJGF>2.0.CO;2](https://doi.org/10.1644/1545-1542(2003)084<0263:PBOJGF>2.0.CO;2)
- Suzuki, K. K., & Ando, M. (2017). Seasonal changes in activity patterns of Japanese flying squirrel *Pteromys momonga*. *Behavioural Processes*, **143**, 13–16. <https://doi.org/10.1016/j.beproc.2017.08.003>
- Vallejo-Vargas, A. F., Sheil, D., Semper-Pascual, A., Beaudrot, L., Ahumada, J. A., Akampurira, E., Bitariho, R., Espinosa, S., Estienne, V., Jansen, P. A., Kayijamahe, C., Martin, E. H., Lima, M. G. M., Mugerwa, B., Rovero, F., Salvador, J., Santos, F., Spironello, W. R., Uzabaho, E., & Bischof, R. (2022). Consistent diel activity patterns of forest mammals among tropical regions. *Nature Communications*, **13**(1), 1. <https://doi.org/10.1038/s41467-022-34825-1>

- Van Schaik, C. P., & Griffiths, M. (1996). Activity periods of Indonesian rain Forest mammals. *Biotropica*, **28**(1), 105–112. <https://doi.org/10.2307/2388775>
- Wickham, H. (2007). Reshaping data with the reshape package. *Journal of Statistical Software*, **21**(12), 1–20.
- Wickham, H. (2016). *ggplot2: Elegant graphics for data analysis*. Springer-Verlag.
- Wickham, H., Averick, M., Bryan, J., Chang, W., McGowan, L. D., François, R., Grolemund, G., Hayes, A., Henry, L., Hester, J., Kuhn, M., Pedersen, T. L., Miller, E., Bache, S. M., Müller, K., Ooms, J., Robinson, D., Seidel, D. P., Spinu, V., ... Yutani, H. (2019). Welcome to the tidyverse. *Journal of Open Source Software*, **4**(43), 1686. <https://doi.org/10.21105/joss.01686>
- Wickham, H., François, R., Henry, L., Müller, K., & Vaughan, D. (2023). *Dplyr: A grammar of data manipulation*. R package version 1.1.4. <https://CRAN.R-project.org/package=dplyr>
- Wilke, C. (2020). *Cowplot: Streamlined plot theme and plot annotations for 'ggplot2'*. R package version 1.1.1. <https://CRAN.R-project.org/package=cowplot>
- Wright, K., & Edwards, M. S. (2009). Considerations for kinkajou captive diets. *Veterinary Clinics of North America: Exotic Animal Practice*, **12**(2), 171–185. <https://doi.org/10.1016/j.cvex.2009.01.008>
- Wright, K. A., Biondi, L., Visalberghi, E., Ma, Z., Izar, P., & Fragaszy, D. (2019). Positional behavior and substrate use in wild adult bearded capuchin monkeys (*Sapajus libidinosus*). *American Journal of Primatology*, **81**(12), e23067. <https://doi.org/10.1002/ajp.23067>
- Youlatos, D., & Gasc, J. P. (2001). Comparative positional behaviour of five primates. In F. Bongers, P. Charles-Dominique, P.-M. Forget, & M. Théry (Eds.), *Nouragues: Dynamics and plant-animal interactions in a Neotropical rainforest* (pp. 103–114). Springer. https://doi.org/10.1007/978-94-015-9821-7_9
- Youlatos, D., & Guillot, D. (2015). Howler monkey positional behavior. In M. M. Kowalewski, P. A. Garber, L. Cortés-Ortiz, B. Urbani, & D. Youlatos (Eds.), *Howler Monkeys* (pp. 191–218). Springer. https://doi.org/10.1007/978-1-4939-1960-4_8
- Youlatos, D., Michael, D. E., & Tokalaki, K. (2008). Positional behavior of Siberian chipmunks (*Tamias sibiricus*) in captivity. *Journal of Ethology*, **26**(1), 51–60. <https://doi.org/10.1007/s10164-006-0029-5>
- Zhu, W. W., Garber, P. A., Bezanson, M., Qi, X.-G., & Li, B.-G. (2015). Age- and sex-based patterns of positional behavior and substrate utilization in the golden snub-nosed monkey (*Rhinopithecus roxellana*). *American Journal of Primatology*, **77**(1), 98–108. <https://doi.org/10.1002/ajp.22314>