Selection and spatial arrangement of rest sites within northern tamandua home ranges

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Abstract

The distribution of suitable rest sites is considered to be a key determinant of spatial patterns in animal activity. However, it is not immediately evident which landscape features satisfy rest site requirements or how these sites are configured within the home range. We used Global Positioning System (GPS)/accelerometer telemetry to investigate rest site selection at the home-range scale for northern tamanduas *Tamandua mexicana* on Barro Colorado Island (BCI), Panama. We developed models specifying each tamandua as the individual experimental unit and averaged coefficients to produce population-level estimates. Tamanduas had on average 17.8 ($\pm$ 8.1) rest sites within their home range and used 1.36 ($\pm$ 0.51) on any given day. These rest sites tended to be located in the core of tamandua home ranges, with active locations associated with the periphery of the home range. Rest sites were positively associated with (1) a high density of *Attalea butyracea* palm trees; (2) elevation; (3) tall vegetation. There was a slight negative relationship between the distribution of rest sites and slope, and no apparent relationship between rest site selection and relative distance to forest canopy gaps. From focal animal observations, we identified that tamandua rest sites were typically located in trees (90%), with 25% (12 of 49) occurring in palms. We contend that northern tamanduas on BCI selected vegetated arboreal rest sites because of reduced likelihood of detection from terrestrial predators in these sites. Our models identified considerable individual variation in rest site selection, which suggests that the practice of pooling individuals and fitting models at an aggregate level may be inappropriate for certain types of habitat selection research.

Introduction

Resting behavior is one of the most prominent and important components of animal ecology, with diverse fitness consequences (Anderson, 1998; Lima *et al.*, 2005). Selection of rest sites can lower predation/parasitism risk (e.g. Buskirk, 1984; Newman *et al.*, 2003; Emsens *et al.*, 2013), reduce thermoregulatory costs (e.g. Thirgood & Hewson, 1987; Mourão & Medri, 2007), maintain social bonds or territories (Doncaster & Woodroffe, 1993; Endries & Adler, 2005), and maximize access to food or water resources (Anderson, 1998; Li *et al.*, 2011). Despite the importance of resting behavior, it is not immediately evident which landscape features satisfy rest site requirements for species that do not construct their own shelters or burrows. The physical characteristics of refuges from predation can include subterranean or elevated (arboreal) position (Lesku *et al.*, 2006; Pruetz *et al.*, 2008), thick vegetative cover or rugged terrain such as steep slopes, all of which reduce visibility to predators or impede predator access (Lesmeister, Gompper & Millspaugh, 2008). In both tropical and temperate environments, animals may choose rest sites for their physical comfort: avoiding exposed sites such as bare branches and hilltops and choosing enclosed sites (valleys, hollow logs, abandoned burrows, caves, tree cavities, thick vegetation) that insulate against wind, rain and temperature extremes and reduce the energy needed to maintain

homeostasis (Schmid, 1998; Mourão & Medri, 2007; Smith et al., 2007; Fei et al., 2012). Location of rest sites can also be influenced by reproductive state, compelling individuals to choose safer sites when young are present, leading to sex-specific usage patterns (Zielinski et al., 2004; Smith et al., 2007). Regardless of the selection pressure, availability of appropriate rest sites could be a primary constraint on the spatial distribution of active behaviors (Doncaster & Woodroffe, 1993). Therefore, identifying the distribution of rest sites is a key step towards understanding habitat suitability, spatial distribution and movement ecology of species that depend on pre-existing shelters for safety (Kappeler, 1998; Lutermann, Verburgt, & Rendigs, 2010).

Traditionally, the spatial distribution of rest sites has been estimated from visual observation (Bowman et al., 2000). With the advent of telemetry technology, rest sites were often inferred from time of day and clusters of consecutive telemetry signals in approximately the same location (Spencer, 1987; Zalewski, 1997; Cavalcanti & Gese, 2010). Recent advances in accelerometry have enabled more precise remote measurement of animal behavior (Wilson, Shepard & Liebsch, 2008; Shepard et al., 2010). Acceleration waveforms are moment-by-moment records of body movement that can reveal foraging, locomotion and resting behavior (Yoda et al., 2001; Mitani et al., 2010). If combined with remotely sensed location estimates [via Global Positioning System (GPS), magnetometers or depth sensors], these biotelemeters can record the spatial distribution of different behaviors, including locations where animals rest.

Neotropical anteaters (Order Xenarthra; Family Myrmecophagidae) have two characteristics that suggest that availability of suitable rest sites is a main determinant of their distribution in the landscape. They are specialized predators of low-quality insect prey (Redford & Dorea, 1984) with correlated lower body temperatures and lower metabolic rates than other mammals of comparable size (McNab, 1985). Due to energy conservation demands associated with this low-quality diet, anteaters enter shallow torpor when at rest (Fernandes & Young, 2008). In this state, they are particularly vulnerable to predation (Montgomery & Lubin, 1977; Smith et al., 2007). Second, depressed metabolic rates limit anteaters' ability to maintain constant body temperature without a considerable expenditure of energy (McNab, 1985). They are therefore expected to seek out rest sites that minimize heat loss to the environment (Camilo-Alves & Mourão, 2006; Mourão & Medri, 2007). Anteaters do not excavate dens and make use of existing environmental features for rest sites such as liana tangles and the burrows of other species (Emmons & Feer, 1990). In the genus Tamandua, body size (4–6 kg) and short pelage put them at risk for predation and temperature sensitivity, respectively (McNab, 1985; Caro, 2005). Despite the expected importance of rest site selection for these species, this behavior remains poorly understood.

Here, we assessed the rest site selection of northern tamandua Tamandua mexicana in Panama. Our aims were to (1) determine the spatial configuration of rest sites within tamandua home ranges and (2) identify environmental covariates that distinguish rest sites from areas where tamanduas are active. We hypothesized that tamanduas would select rest sites with physical characteristics that minimize detection and access by terrestrial predators and reduce exposure to the prevailing weather conditions. Specifically, we predicted that rest sites would be arboreal and associated with taller trees (increased vegetation height) and steeper slopes for predator avoidance, and that rest sites would be associated with lower elevations and avoidance of forest gaps as a means of thermoregulation.

Methods

Study area and species

We examined the rest site selection of tamanduas on Barro Colorado Island in the Republic of Panama (BCI; 9°9′N, 79°51′W), which has been extensively described elsewhere (Dietrich, Windsor & Dunne, 1982). Briefly, the island has an average annual temperature of 27°C (± 9°C) and a broad, flat central plateau with steep ridges and valleys (20–30° slopes) covered in a semi-deciduous tropical forest mosaic of old growth (≥2000 years old) and secondary growth (≥100 years old; Leigh, 1999). The tropical climate does not vary greatly in daily or seasonal temperature, but there are periodic intense rain and wind events that can increase mammalian body heat loss to the environment (Thies, Kalko & Schnitzler, 2006).

The distribution of northern tamandua (hereafter 'tamandua') extends from southern Mexico to north-western Peru (Nuñez-Perez et al., 2011). Within this range, the species occurs below 1000 m in a variety of forest and woodland habitats (Navarrete & Ortega, 2011). Despite being ant and termite specialists, northern tamanduas on BCI and the surrounding mainland also consume ripe fruits of the palm Attalea butyracea (Brown, 2011). They are sexually monomorphic, solitary (apart from females with dependent young), and reproduction is aseasonal (Lubin, 1983). Territoriality has not been confirmed in this species.

Tamanduas have a prehensile tail and move equally well arboreally and terrestrially (Montgomery & Lubin, 1977). They are generally reported to rest in trees and tree cavities, vine tangles and on the ground in abandoned burrows (Emmons & Feer, 1990). On BCI, tamanduas are subject to predation primarily from resident ocelots Leopardus pardalis as well as puma Puma concolor and jaguar Panthera onca that visit the island regularly (Moreno, Kays & Samudio, 2006). Whereas ocelots can and do climb trees, all three cats are reported to primarily pursue terrestrial prey (Moreno et al., 2006; Cavalcanti & Gese, 2010). The only confirmed aerial predator of tamanduas (harpy eagle Harpia harpyja) has been absent from BCI for at least 50 years (Rettig, 1978; Touchton, Hsu & Alleroni, 2002).

Animal capture and telemetry

Between December 2008 and March 2010, we captured 17 northern tamanduas using snare poles (Ketch-all, San Luis Obispo, CA, USA) or a dart rifle and net (model 178B, Pneu-

Dart, Williamsport, PA, USA). Animals were sexed and given ear tags for future identification. We fitted tamanduas with 60-g telemetry tags ($63 \times 70 \times 13$ mm; 1–2% of body weight) attached to the lower back using 5-min epoxy (Devcon, Danvers, MA, USA). All capture, tagging and monitoring protocols were approved by the Institutional Animal Care and Use Committees of the University of California, Davis and the Smithsonian Tropical Research Institute.

The GPS/accelerometry tags (e-obs GmbH, Grünwald, Germany) contained a tri-axial accelerometer, an ultra-high frequency (UHF) radio transmitter and a GPS microchip (U-Blox LEA-4S). Tag accelerometers recorded at 18.74 Hz in a short (~3 s) burst every 120 s. The tags recorded GPS locations at intervals between 300 and 4000 s (for schedule justification and details, see Brown *et al.*, 2012). This collection interval was not expected to affect data calculations because our analysis does not require consistent intervals between locations, but only that both active and resting locations were adequately sampled. We calculated GPS location error using a large sample average from stationary deployment tests and immobile study animals. Spatially distinct rest sites were identified when the linear distance between resting locations exceeded the average location error documented in our system ($\bar{x} = 20 \pm 6.5$ m).

Determination of active and resting locations

We visually observed tamanduas one to three times weekly during diurnal hours after locating them using the UHF tracking beacon. We conducted instantaneous focal animal observations at 120-s intervals (Altmann, 1974). Observing the animals on the same schedule as the accelerometer recordings allowed us to reliably assign active or resting status to accelerometer output (see below). Active behaviors included foraging (opening and feeding from insect nests) or locomotion (climbing or walking along branches or the ground). Rest behavior included sleep (eyes closed or head tucked), grooming or sitting motionless while vigilant (eyes open). During animal observations, we also recorded resting location (burrow, branch, palm, etc.) of both focal animals and untagged individuals encountered opportunistically.

In this study, we used acceleration records of the axis measuring side-to-side acceleration along the horizontal body plane to differentiate between resting and active behaviors. With focal observations, we validated that accelerometer records with high variance of the burst measurements indicated active tamandua behavior, whereas records with low burst variance reflected inactive behavior. We used a variance threshold for categorizing each accelerometer burst as active or resting (98% accurate; sensitivity = 97.2%; specificity = 98.7%; Altman & Bland, 1994; Brown *et al.*, 2012). We assigned bursts that were recorded within ~8 min of each GPS location and categorized the *GPS location* as a resting location if more than 50% of those bursts met the variance threshold for resting. During active behaviors such as foraging, tamanduas were rarely motionless for more than a minute, so

it is unlikely that locations categorized as 'resting' were only temporary stops in an otherwise active period.

Utilization distributions

To document the distribution of rest sites within the home range, we developed utilization distributions (UDs) for each individual tamandua from the GPS telemetry locations (Kernohan, Gitzen & Millspaugh, 2001; Gitzen, Millspaugh & Kernohan, 2006). We calculated these UDs in R 2.10.0 (R Development Core Team, 2011) for each tamandua at a resolution of 1 m. We converted the UD values to percent volume contours at 1% intervals (Marzluff *et al.*, 2004; Montgomery, Roloff & Millspaugh, 2012, 2013) using ArcMap 10.0 (Environmental System Research Institute, Redlands, CA, USA). The 1st UD percentile represented the core of the home range, whereas the 100th percentile defined the periphery. We then used *t*-tests to examine if resting and active locations were distributed within different regions of the UD (based on UD percentiles).

Environmental covariates

We developed a suite of five abiotic and biotic characteristics describing the environment on BCI and compared these features with spatial patterns of tamandua active and resting behavior. These environmental covariates were based on geospatial data provided by the Smithsonian Tropical Research Institute (available from http://mapserver.stri.si.edu/geonetwork/srv/en/main.home). We used a digital elevation model (at a 10-m resolution) to portray elevation (range 0–175 m) across BCI and to calculate slope (range 0–42°) measured in degrees. From LiDAR mapping (1-m resolution), we described the height of the vegetation structure on BCI (Lobo and Dalling, unpubl. data). Canopy gaps within 20 m of the shoreline, which resulted from the absence of vegetation cover over water, were eliminated from consideration. We calculated distance to canopy gaps (range 0–350 m) that were apparent at 10 m off the ground and covered an area of >100 m². Due to the complex shoreline of the island, we calculated the distance that accounted for the natural obstacles (e.g. bays and inlets) to terrestrial movement. We also mapped the density of *Attalea* palm trees at a 50-m resolution (range 0–7) based on data delineating these trees across BCI (Garzon-Lopez *et al.*, 2014).

Population-level rest site selection model

We fit generalized linear mixed models (GLMM) to predict rest site selection within the home range as a function of environmental covariates. We specified each tamandua as the individual experimental unit and averaged coefficients to produce a population-level model (e.g. Marzluff *et al.*, 2004; Millspaugh *et al.*, 2006; Sawyer, Kauffman, & Neilson, 2009). The dependent variable was binary, where 1 refers to resting locations and 0 refers to active locations documented for each tamandua via GPS/accelerometry. We coded this model in SAS Proc GLIMMIX (SAS Institute, Cary, NC, USA), with a

logit link function specifying the intercept as the *subject* of the model to identify that all observations derived from the same individual (Littell *et al.*, 2006). We included a spatial autocorrelation component to account for dependencies in the distribution of telemetry locations across space, and a temporal autocorrelation component to account for dependencies across time. This temporal autocorrelation component accounted for the uneven GPS sampling intervals (300–4000 s). Treating each animal as the individual experimental unit has several distinct advantages (see Sawyer *et al.*, 2009). Specifically, models run at the level of the individual animal can better incorporate spatial and temporal autocorrelation and can better depict the impact of individual variation on the model coefficients (Marzluff *et al.*, 2004; Millspaugh *et al.*, 2006; Thomas & Taylor, 2006; Sawyer *et al.*, 2009).

Model selection is complex for mixed-effects models due to the type of estimation method (Gillies *et al.*, 2006; Hebblewhite & Merrill, 2008; Koper & Manseau, 2009). Thus, we fit these models using maximum likelihood estimation to enable model selection via information theoretic approaches and then used restricted maximum likelihood for estimation of the regression coefficients (cf. Mardia & Marshall, 1984; Bonnot, Schulz & Millspaugh, 2011). We developed models from all possible combinations of the five environmental covariates. We evaluated model parsimony using the Akaike information criterion (AIC) and ranked model performance using AIC weights (Burnham & Anderson, 2002). If additional models were within 1/8th ω_i of the top-ranking model, we model-averaged the parameter estimates from the top-ranking models (Bonnot, Rumble & Millspaugh, 2008). Finally, we averaged the coefficients of top-ranking models among individuals to plot the magnitude of effects at the population level (cf. Marzluff *et al.*, 2004).

Results

We collected a total of 8189 telemetry locations from 17 individuals (8 males and 9 females) between 2008 and 2010. Not all individuals were studied concurrently and we were not able to capture all tamanduas living within a given area of the island. Consequently, we did not analyze seasonal differences or spatial overlap between individuals. Telemetry tags were deployed for an average of 13.4 days (range 6–20) before falling off the tamanduas (typically via grooming behavior; Table 1). The average number of locations per individual was 483 (range 128–1064; Table 1). Locations were approximately evenly divided between resting ($n = 3782$) and active ($n = 4407$) behaviors.

We conducted 138 h of focal behavioral observations of tagged tamanduas ($\bar{x} = 8.1 \pm 5$ h per individual; Table 1). During these observations, we directly recorded 49 rest sites: 19 from tagged males, 25 from tagged females and 5 from untagged tamanduas. Most of these sites (17 of 49 or 35%) were on thick horizontal tree limbs. Twelve rest sites (25%) were in *Attalea* palms, 5 (10%) were in liana tangles and 5 (10%) were either in terrestrial logs or burrows. One tagged tamandua was observed entering a hollow in a tree for rest. For the remaining nine sites (18%), we determined that tamanduas were resting in an arboreal position but could not distinguish whether they were using tree limbs, tree hollows or liana tangles. Among these directly observed rest sites, females used *Attalea* palms significantly more than males (Fisher's exact test $P = 0.0007$).

Tamandua home ranges averaged 25.3 ha (sᴅ = 14.9 ha; Table 1). Tamanduas had on average 17.8 (± 8.1) rest sites within their home ranges and used a mean of 1.36 (± 0.51) rest sites per 24-h period with no detectable differences based on

Table 1 Summary of the number of telemetry locations, resting locations, distinct rest sites, and days monitored for tamandua anteaters *Tamandua mexicana* on Barro Colorado Island, Panama, 2008–2010

Sex	ID	Hours of observation (h)	Telemetry locations (*n*)	Resting locations (*n*)	Distinct rest sites (*n*)	Days monitored (*n*)	Area of UD (ha)
Male	192	0.53	317	214	23	13.8	32.08
Male	195	10.8	252	147	19	8.1	29.84
Male	197	8.7	128	64	13	11.8	34.68
Male	1167	10.8	345	224	11	10.9	13.92
Male	1170	14.4	744	610	28	16.5	16.87
Male	1173	4.5	418	78	13	10.3	38.55
Male	1176	3.3	499	56	7	6	11.22
Male	5462	6.6	744	576	24	13.1	14.27
Female	187	8.2	411	198	22	17.7	24.97
Female	193	10.9	313	69	12	8.9	12.08
Female	194	3.5	583	271	31	14.9	67.34
Female	1169	3.7	133	17	2	13.4	17.13
Female	1171	13.4	205	88	13	14.1	22.12
Female	1193	12.9	938	668	30	18.7	12.76
Female	1174	18.9	1064	217	15	16.2	19.94
Female	1175	5.8	943	198	20	19.7	16.94
Female	5461	1.7	152	87	19	11	46.06

The area (in ha) of the 100% utilization distribution (UD) home range for each individual is also presented.
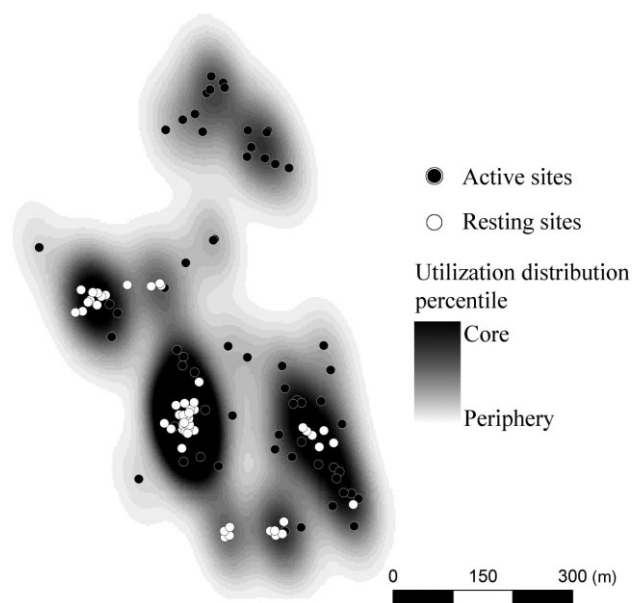
Figure 1 The distribution of active and rest sites within the home range [or utilization distribution (UD)] of one tamandua anteater *Tamandua mexicana* (ID = 197) that was tracked using Global Positioning System (GPS) telemetry on Barro Colorado Island, Panama, in 2009. The UD was calculated using a bivariate plug-in matrix that calculated bandwidth along rotated axes based on 128 GPS locations.

Figure 2 The relative distribution of active and rest sites within the home ranges of individual tamanduas *Tamandua mexicana* tracked on Barro Colorado Island, Panama, from 2008 to 2010. The points represent average metrics for each individual tamandua of utilization distribution (UD) percentiles at active and rest sites. The 1st UD percentile corresponds to the core of the home range, whereas the 100th percentile corresponds to the periphery. Averaged UD percentiles among all tamandua for both active and rest sites are portrayed with the hatched lines.

sex or home-range size (Table 1). Examination of the UDs revealed that tamanduas used different portions of their home ranges when active compared to when resting. Specifically, tamanduas tended to rest near the core of their home range and be active in the periphery of their home range (Figs 1 and 2). Across all individuals, active locations occurred on average in the 72nd UD percentile, whereas rest locations occurred on average in the 41st UD percentile (Fig. 2). Thus, resting and active behaviors were separated by an average of 31 UD percentiles (Mann–Whitney adjusted *H*-statistic = 22.1, $P < 0.001$). The spatial positions of active and rest sites within the home ranges were significantly different for all individuals (see Supporting Information Table S1).

We considered the influence of five environmental covariates on rest site selection which led to a total of 31 possible models for consideration per animal. None of the environmental covariates were collinear (i.e. $|r| > 0.5$) and so our set of all possible combinations included 527 models (31×17 individual tamanduas). All of the environmental covariates under consideration were featured in at least four top-ranking mixed-effects models (Table 2). The mean dispersion parameter for top-ranking models was 0.64 (SD = 0.08), indicating that the data were not overdispersed. We found that, on average, tamanduas rested in habitat that was at higher elevation, with greater vegetation height, and more *Attalea* palms than habitat that they used when active (Fig. 3). Slope and distance to canopy gaps differed slightly between the selection of resting and active habitat. We also found
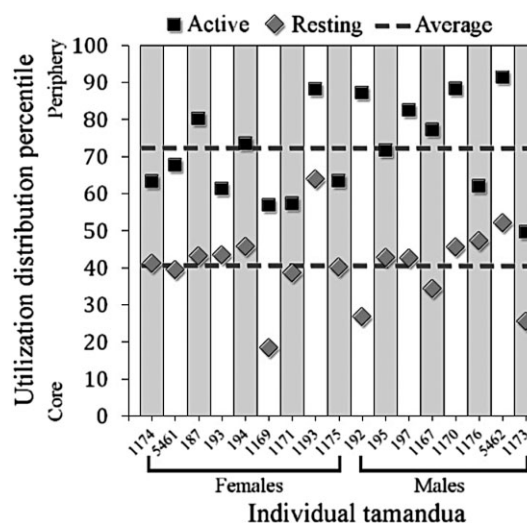
considerable individual variation among the parameter estimates within the top-ranking models, and this variation did not appear to aggregate by sex (Table 2).

Discussion

With GPS/accelerometer telemetry, we quantified spatial patterns in tamandua resting behavior that previously could only be described inferentially. Specifically, we identified the importance of arboreal resting sites and an association with *Attalea* palm trees in this population of tamanduas. Additionally, we discovered that tamanduas tended to use the peripheries of their home ranges when active and the cores of their home ranges for rest, emphasizing the importance of high-quality rest sites for their movement ecology. Similar patterns of space use have been observed in wolves *Canis lupus* in Italy where animals retreat to the core of their home range for rest and travel from these sites to the periphery of their home range when actively foraging (Ciucci *et al.*, 1997). Tamanduas also used multiple rest sites within their home range, typically changing sites every night. By doing so, they possibly minimized travel distance to a greater part of their home ranges (Smith *et al.*, 2007) while also reducing the probability that predators would become conditioned to their location (Emsens *et al.*, 2013). What remains unclear is whether there is intraspecific competition for suitable rest sites among tamanduas, and if such competition influences the spatial distribution and configuration of home ranges. In other

Table 2 Generalized linear mixed regression parameter estimates and standard errors (SE) for the environmental covariates featured in the final models explaining northern tamandua anteater *Tamandua mexicana* rest site selection on Barro Colorado Island, Panama, 2008–2010

| Sex | ID | Parameter estimates (SE)[a] | | | | |
		DEM	Palm trees	Veg. height	Slope	Gaps
Male	192	–	0.652 (0.23)	0.055 (0.03)	–	–
Male	195	–	–	–	–	0.0002 (0.01)
Male	197	–	–	0.011 (0.03)	–	–
Male	1167	0.073 (0.04)	–	–	–	–
Male	1170	–	–	–	–0.011 (0.02)	–
Male	1173	–	–	–	–	–0.003 (0.01)
Male	1176	–	–	0.030 (0.02)	–	–
Male	5462	–	–	–	–0.087 (0.04)	–
Female	187	–	–	–	–	0.009 (0.00)
Female	193	–0.001 (0.03)	–	–	–	–
Female	194	0.016 (0.01)	–	–	–	0.001 (0.01)
Female	1169	–	–	–0.029 (0.04)	–	–
Female	1171	–	–	–	–	–0.022 (0.01)
Female	1174	–0.005 (0.01)	0.237 (0.13)	–	–0.001 (0.02)	–
Female	1175	–	0.218 (0.12)	–	0.017 (0.05)	0.009 (0.01)
Female	1193	–	0.149 (0.17)	–	–	–
Female	5461	–	0.034 (0.17)	–	–0.035 (0.07)	–

[a]Three of the five environmental covariates were measured in meters including elevation (*DEM*), vegetation height (*Veg. Height*) and distance to canopy gaps (*Gaps*). Slope (*Slope*) was measured in degrees and density of *Attalea* palm trees (*Palm trees*) was the count of palm trees across Barro Colorado Island at a 50-m resolution.

mammals, the availability of suitable rest sites can constrain home-range size (Doncaster & Woodroffe, 1993) and can be a limiting factor in population growth (Lutermann *et al.*, 2010). The large number of sites that tamanduas used over the relatively short tracking period does not suggest that quality rest sites are limiting in this forested habitat; however, our experimental design did not allow for a systematic examination of these effects and we anticipate this as an opportunity for future research.

The three covariates that had the greatest effect on population-level rest site selection by tamanduas were the density of *Attalea* palm trees, vegetation height and elevation. Rest site selection was positively associated with all three covariates. These results are consistent with many other studies of mammalian rest site ecology. Elevated resting position (ridges, cliffs, tall trees) reduces detection and access by terrestrial predators (Pruetz *et al.*, 2008; Li *et al.*, 2011; Fei *et al.*, 2012; Wam, Eldegard & Hjeljord, 2012). Free-ranging southern tamanduas *Tamandua tetradactyla* were observed sleeping in the crowns of palms *Copernicia tectorum* and other trees in Venezuela (Montgomery, 1985). *Attalea* and other palm species are used as rest sites by a wide range of mammals besides tamanduas, including kinkajous *Potos flavus* (Kays & Gittleman, 1995), mouse opossums *Micoureus demerarae*; Morães & Chiarello, 2005) and several primates (Heymann, 1995; Puertas, Aquino, & Encarnacion, , 1995; Zhang, 1995; Schreier & Swedell, 2008). *Attalea* are tall (>10 m) trees with smooth bark, dense foliage and no side branches, and are likely selected for rest because these characteristics present visual and physical obstacles to terrestrial predators (Duarte & Young, 2011). We interpret this tendency to select resting

habitat at high elevations with taller vegetation and a greater density of (tall) palm trees to be indicative of predator avoidance in this tamandua population. Although some individuals in this population do consume palm fruits (Brown, 2011), fruits are only seasonally available and therefore unlikely to influence rest site selection across the study period.

The tree canopy of BCI is heavily vegetated year-round (Leigh, 1999). We suspect that resting in tree canopies also buffered tamanduas against fluctuations in ambient temperature. Giant anteaters *Myrmecophaga tridactyla* monitored in the southern Pantanal chose forest patches for rest because they were cooler than open habitats during the hot hours of the day and warmer during the cool hours (Mourão & Medri, 2007). On BCI, even though temperatures do not vary to extremes, ambient temperature recorded at weather stations on the island fluctuated an average of 2°C less under the canopy compared to temperatures recorded at exposed sites (weather data publicly available from http://biogeodb.stri.si.edu/physical_monitoring/research/). At lower ambient temperatures, tamanduas would need to invest energetic resources into maintaining adequate body temperature while at rest. When ambient temperatures are high, the depressed body temperature that permits shallow torpor and energy savings in anteaters would be difficult to maintain (Schmid, 1998). Although tamanduas used higher elevations for rest, contrary to our predictions under the thermoregulation hypothesis, rest sites protected by foliage or inside tree cavities may compensate for the greater exposure to the elements that exists on hilltops. This speculation is further supported by the model results showing that rest sites tended to be away from canopy gaps. Canopy gaps have higher variation in ambient temperature plus greater
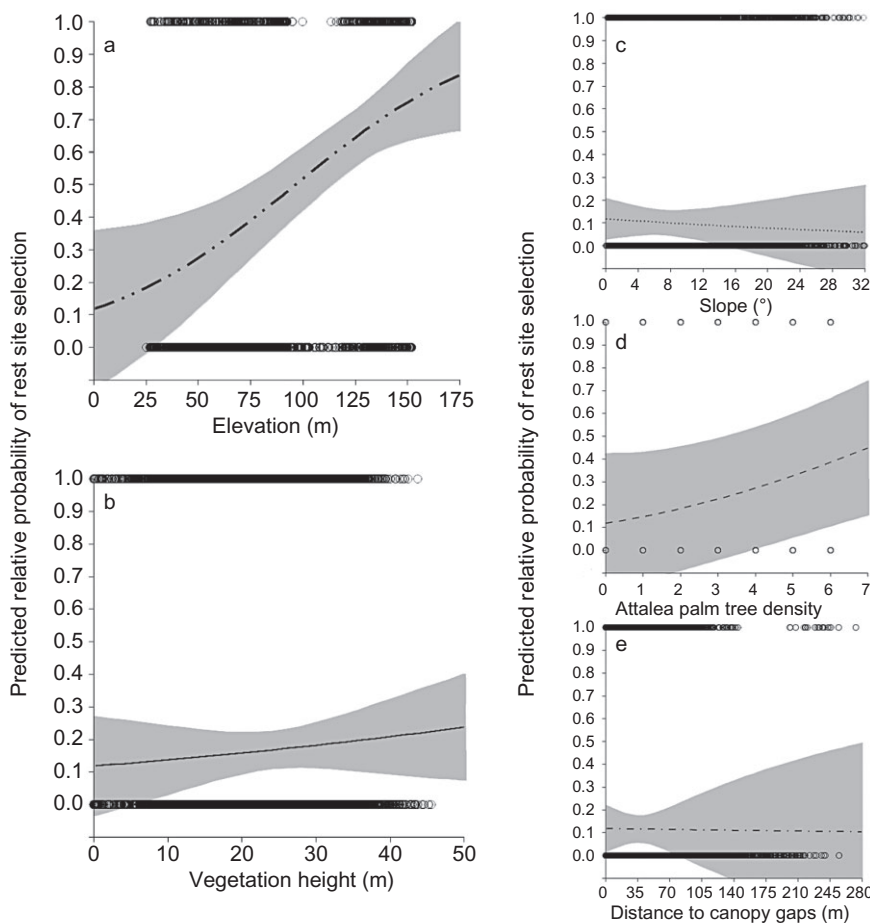
Figure 3 Panels (a)–(e) show the predicted relative probability of rest sites for tamanduas *Tamandua mexicana* in relation to five environmental covariates on Barro Colorado Island, Panama (2008–2010). Each regression is plotted to the maximum value of the data distribution for that specific environmental covariate. Gray shading depicts the 95% confidence interval of the estimated coefficients, whereas open circles show the raw data used in each model. The horizontal axis of panel (d) depicts an index of *Attalea* palm tree density (see main text for full description).

exposure to rainfall and wind which would leave tamanduas vulnerable to losing body heat while asleep (Thies *et al.*, 2006). An alternative explanation is that the shorter and generally younger vegetation found in forest gaps (Helmer *et al.*, 2010) does not provide protection from predation for tamanduas, as discussed above and below.

Our focal animal observations largely corroborated our regression modeling results. We observed that tamandua rest sites were predominantly arboreal, associated with *Attalea* palms, and protected either by substrate or vegetation structure. Use of protected sites for rest supports both the thermoregulation hypothesis and the anti-predator hypothesis. In the closed-canopy forests of BCI, arboreal rest sites can be at least partially obscured by the vegetation of the lowest stratum of a tall canopy and can visually hide species from terrestrial predators (e.g. Wright, 1998). This is supported by the fact that nearly 20% of arboreal rest sites used by tagged tamanduas could not be pinpointed by eye. Resting on a bare branch (one-third of visually recorded rest sites) does not reduce heat loss, but can reduce predation risk if tamanduas are relying on crypsis through immobility, as is hypothesized for taxonomically diverse prey species (Ruxton, Sherratt & Speed, 2004). A minority of the rest sites that we observed (5 of 49) were located terrestrially. Tamanduas are known to rest

in burrows: a Brazilian study of translocated *T. tetradactyla* reported sleeping locations to be entirely terrestrial (Rodrigues & Marinho-Filho, 2003). Subterranean burrows (like dense vegetation) can also provide protection against wind, rain and temperature extremes (Schmid, 1998; Lesmeister *et al.*, 2008). However, we suspect that the majority of tamanduas on BCI avoided these rest sites given prevailing risk of terrestrial predation from multiple felids (ocelot, puma and jaguar). Furthermore, females were never observed resting on the ground. We only observed females entering *Attalea* palms for rest, and one pregnant female and another female with a young calf were observed to rest exclusively in palms. Sex difference in resource use is a common phenomenon among mammals (Zielinski *et al.*, 2004; Mooring *et al.*, 2005; Martin & Martin, 2007). Tamanduas are not obviously sexually dimorphic (Navarrete & Ortega, 2011), but since they show maternal-only care and calves are more vulnerable to predation than adults, this apparent sex-bias in palm use reinforces the premise that BCI tamanduas choose rest sites based on predation risk and suggests that female tamanduas may be more risk-averse than males (Smith *et al.*, 2007; Ciuti & Apollonio, 2008).

While we averaged estimates to develop population-level inferences of rest site selection, we documented variation at

the level of individual tamanduas with respect to elevation, slope and distance to canopy gaps (Table 2). However, the relationship between rest site selection and density of *Attalea* palms was positive in all cases. This further highlights the importance of *Attalea* palms in the rest site selection of tamandua anteaters. Additionally, tamandua selection of rest sites and vegetation height was largely consistent with three of the four parameter estimates being positive. In habitat selection research, animals are commonly grouped by age, sex, reproductive state and/or season, and models are evaluated at that aggregate level (Spencer, 1987; Martin & Martin, 2007; Wilson & Nielsen, 2007; Lutermann *et al.*, 2010). When run at the aggregate levels, the variation between animals is masked by the experimental design (Thomas & Taylor, 2006; Sawyer *et al.*, 2009). The individual variation that we documented in this analysis suggests that the process of pooling individuals and running models at an aggregate level without explicit consideration of individual variation might be inappropriate for the examination of certain ecological questions. This variation may ultimately be linked to life-history stage; however, we propose that a much larger sample size and considerably longer observation period would be necessary to assess this contention. Here, we demonstrated the utility of short-term, high-resolution telemetry and individualized, spatially explicit models to test broadly applicable hypotheses for why animals select their places of repose. Our hypotheses were not mutually exclusive, but future work should examine the spatial distribution of foraging activity, the timing of activity and rest, and the temporal pattern of rest site reuse to tease apart the relative contributions of predation risk, temperature and food availability to variation in tamandua home-range sizes and movement patterns.

Acknowledgements

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Supporting information

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

Table S1. The distribution of active and resting locations within the home range of 17 individual tamanduas (ID) tracked with GPS/accelerometer tags on Barro Colorado Island, Panama, 2008–2010. Average utilization distribution (UD) percentiles are presented, with 1 corresponding to the core and 100 corresponding to the periphery of the home range. *T*-statistics for the *t*-test of unequal variances and the corresponding *P*-values are also provided.