Movement behavior of a tropical mammal: The case of *Tapirus terrestris*

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ABSTRACT

Animal movement characteristics are not species-specific traits, but rather individual features that respond to various selective pressures. To understand patterns of animal movements, it is especially important to explore how they are affected by differences in landscape and habitat configuration. This paper presents an analysis of the movement patterns of a species of conservation concern in Northwest Amazon, the lowland tapir (*Tapirus terrestris*), in relation to landscape elements identified as resource concentration areas (palm stands and natural salt licks). We identify the structure of the movement behavior of a sub-adult male lowland tapir using Behavioral Change Point Analysis (BCPA) and a set of metrics capturing velocity and variance. We also estimate this tapir's Utilization Distribution (UD) using the dynamic Brownian Bridge Movement Model (dBBMM) in order to better understand its trajectories and space-use patterns. Our results provide insights about this animal's movement, making it possible to differentiate between foraging behaviors, characterized by long trips and selective resource use, and explorative behaviors, characterized by short displacements and a notable decrease in the usage of resource areas and its trajectories. The high influence of landscape elements on movement characteristics suggest that tapirs may perceive the Amazonian forest as heterogeneous rather than homogeneous mosaics. Therefore, the study of movement characteristics proves to be useful for the development of future studies and conservation plans.

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1. Introduction

Animal movement is a process by which organisms displace themselves in space and time (Thiebault and Tremblay, 2013), either passively or in response to some behavior or stimulus (Hansson et al., 1995). Movement ecology is a growing discipline that has already made important contributions to population and conservation ecology (Hawkes, 2009). Locomotion is a defining characteristic of most mammal species and is key for understanding their ecology, life history and the impact of changes in environ-mental factors. Animal locomotion is a behavioral response to physiological and environmental conditions (Gurarie et al., 2009), namely body size (Baguette et al., 2013; Bowler and Benton, 2005), reproduction, migration (Hansson et al., 1995), changes in resource spatial distribution, memory of previous experiences (Morales et al., 2010), among others. Most animal movement studies are motivated by population dynamics questions (Gurarie et al., 2009; Hawkes, 2009). Although movement studies focused on individual organisms are less frequent, a number of works at the individual level have been undertaken, mainly addressed at understanding movement as a response to morphology and behavioral change (e.g. the transition to feeding) as a response to resource availability (Spiegel et al., 2017). Understanding individual locomotion helps in inferring the effects of behavior on movement that enables organisms to explore differences in landscape and habitat configuration (Gurarie et al., 2009).

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Movement behavior depends not only on life history traits, but also on other drivers such as fine scale spatial heterogeneity perception, landscape dynamics (Bowler and Benton, 2005; Hawkes, 2009), and the spatial distribution of resources (Kadoya, 2009), thus affecting not only individual performances but also population dynamics (Morales et al., 2010). The movement distance of a given species is associated with activities such as breeding and feeding (Hansson et al., 1995) or refuge location (Hawkes, 2009).

Recently, global positioning system (GPS) telemetry has contributed greatly to animal movement research, making it possible to obtain detailed movement information about wild animals in their natural habitat (Cagnacci et al., 2010; Gurarie et al., 2009; Hebblewhite and Haydon, 2010; Morales et al., 2010, 2004). GPS technology has permitted the tracing of positions and movement of animals and the transfer of this data remotely (Urbano et al., 2010). It has also made it possible to locate the spatial position of an individual at short time intervals, allowing for the reconstruction of movement trajectories (Hebblewhite and Haydon, 2010; Morales et al., 2010). These techniques facilitate the exploration and comprehension of habitat use, displacement patterns and landscape connectivity (Cagnacci et al., 2010; Hebblewhite and Haydon, 2010; Morales et al., 2010, 2004). All of this ecological knowledge is helpful for the management and effective conservation of a large number of mammal populations. Nevertheless, movement data analysis is not an easy task, with particular complications arising from spatial and temporal autocorrelation (Gurarie et al., 2009; Hebblewhite and Haydon, 2010; Urbano et al., 2010). This difficulty has motivated the development of different analytic and statistical techniques to represent and analyze movement. Recent approaches incorporate the temporal structure of the data, providing better information on things like location frequency and movement rates through different landscape elements (Benhamou, 2011; Watts et al., 2015).

Utilization distributions (UD) are widely used to study home ranges (Watts et al., 2015; Worton, 1989). One of the most widely used approaches to estimate the utilization distribution of an organism is based on simple kernel densities that do not account for temporal structure (Kranstauber et al., 2014). The Brownian Bridge Movement Model (BBMM) and dynamic Brownian Bridge Movement Model (dBBMM) improve on the kernel density approach by considering the sequential organization of locations and the amount of time spent between them, modelling explicitly the movement trajectory and scale (Kranstauber et al., 2014, 2012). Additional approaches, such as the Behavioral Change Point Analysis (BCPA), help in exploring the structure of movement behavior. BCPA places a moving window over the trajectory time series to detect significant change points and thereby segment the trajectory into sections that appear to involve different behaviors (Gurarie et al., 2009).

Tapirs are among the most endangered mammals in the Neotropical region. Because of their significant role in seed dispersion (Richard and Juliá, 2000; Salas and Fuller, 1996), tapirs are considered fundamental species for neotropical forest dynamics, holding the potential to generate cascading ecological effects related to the composition, succession and regeneration of plant communities (Bodmer, 1990; Galetti et al., 2001; Henry et al., 2000; O'Farrill et al., 2013; Salas and Fuller, 1996; Tobler et al., 2010). The Amazon forests, inhabited by the lowland tapir (Tapirus terrestris), are one of the most threatened regions of the world but still hold large remaining undisturbed areas that are ideal sites to comprehend the movement and infer the behavior of tapirs in their natural environment. In this paper, we analyzed the small-scale movement of a male sub-adult lowland tapir in the NW Amazon. The objectives of this assessment were to analyze the spatio-temporal variability of the use of space by an individual T. terrestris in this region. We focused on two research questions: 1) What is the spatial and temporal movement pattern of T. terrestris? 2) Is it determined by resource concentration areas?

2. Methods

2.1. Study area

The study was performed in the mid-basin of the Caquetá river, at the indigenous community Nonuya Villazul, Puerto Santander, Amazonas, Colombia (-0.271692 N, -0.936213 S; -72.134745 E, -71.608166 W, Fig. 1). With an approximate extension of 10,000 km^2, this area is part of the Amazonas river basin and it is situated between 150 and 300 m above sea level. The weather is tropical with a mean temperature of 25.7 °C. Precipitation regime is almost unimodal, the area is located in the Tropical Humid Forest (THF) life zone (Duivenvoorden and Lips, 1993). This area is sparsely inhabited by humans, with the larger and more permanent populations being located in Araracuara and Puerto Santander (Duivenvoorden and Lips, 1993). Although there are native communities along the Caquetá river, the forests are highly preserved with various indigenous reserves.

2.2. Data

A sub-adult male lowland tapir (Tapirus terrestris) was captured and equipped with a telemetry collar Telonics® (TGW-4570-3 GPS/Gen4 GPS-Iridium collar system) in July 2014. This collar has a programmable drop-off system and other components for the following functionality: GPS positioning, VHF transmission, data storage, and data transmission using the Iridium Satellite System. The individual was captured by a team of six persons that included a wildlife veterinarian member of UICN/SSC − Tapir Specialist group (TSG) who led the capture process, monitored the tapir's vital signs, and put the collar around its neck. The collar was programmed to work for a period of 7 months, 24 h per day, recording a GPS location every hour from 6:00 to 18:00 (daytime) and every 30 min from 18:00 to 5:59 (nighttime and morning). A total of 5199 location fixes were obtained and used, 2350 daytime and 3400 nighttime and morning. Locations had a mean longitudinal error of 16.7 m, and most of the data had an error of approximately 3–30 m.

The capture process was performed following all applicable international, national and institutional guidelines for the care and use of animals (Mangini, 2007; Mangini et al., 2012). The field phase of this study was conducted under the permission of the National Environmental Authority (reference number 0255 of 2014 – Autoridad Nacional de Licencias Ambientales "ANLA"). The study protocol and field procedures were approved by ANLA and by the animal ethics committee from Universidad Nacional de Colombia.

Tapir movement is likely to be highly determined by the distribution of resource concentration zones. Tapirs are forage/frugivorous animals (Montenegro, 2005) that consume a great diversity of plant species. Feeding includes a high percentage of fruits (Daniel and Brooks, 1997; Lizcano and Cavelier, 2000; Ministerio de Ambiente Vivienda y Desarrollo Territorial – Direcci&n de Ecosistemas y Naturales, 2005), and the animal makes highly selective use of feeding zones, such as Mauritia flexuosa stands (palm stands locally known as cananguchales) in the Amazon (Daniel and Brooks, 1997). Like other mammals, they tend to visit places with high nutrient concentrations, like natural salt licks, where they obtain nutritional benefits and also potentially communicate with other individuals (Montenegro, 1998). Consequently, the study area was surveyed and the geopositions of natural salt licks and M. flexuosa stands were recorded and analyzed alongside the observed movement patterns.
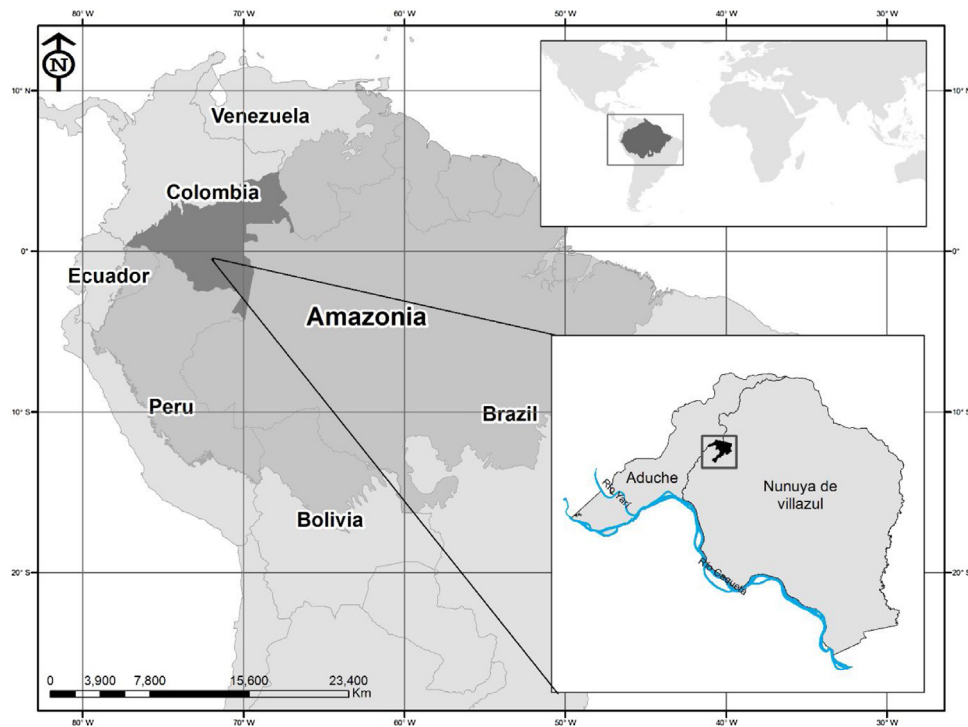
Fig. 1. Location of the study site.

2.3. Data analysis

To describe the tapir's movement, we analyzed the velocity and variability of the movement behavior at a high temporal and spatial resolution (fine scale), identified behavior changes with BCPA analysis, and estimated the UD with a dBBMM. These approaches are appropriate for the assessment of movement at an individual level. All the analysis and plots were done with R v 3.2.1 (R development Core Team 2015) using the "bcpa" package Version 1.1 (Gurarie, 2013) and "move" v. 1.5.514 (Smolla and Kranstauber, 2014) for the development of the BCPA and dBBMM respectively.

2.3.1. Spatial-temporal variability

As a first step, an exploration was made of the spatial and temporal variability of the tapir's activity during the assessment period (7 months). The tapir's activity was evaluated in terms of velocity changes, considering different temporal scales (hours, days and months). The velocity was estimated as the distance travelled and the time spent between each set of two points. A plot of Brownian motion variance over time was constructed to observe movement tortuosity changes, which is a dimensionless parameter used in the dBBMM but also of interest on its own (Kranstauber et al., 2012). The Brownian motion variance was estimated using a window size of 36 (equivalent to a day) and a margin of 12, both parameters selected based on *T. terrestris* biological characteristics, expert criteria, and the suggestions made by the dBBMM software developers. We also tested smaller window sizes but did not find differences in the results.

2.3.2. Behavioral change identification (Behavioral change point analysis: BCPA)

BCPA was used to explore the tapir's movement behavioral structure. BCPA places a sliding window over the time series of a given movement parameter to identify points at which the parameter appears to change (Gurarie et al., 2009). This parameter, which could be velocity persistence or turning angle, is modelled as a Gaussian auto-regressive process continuous in time with mean

(μ), standard deviation (σ) and a characteristic time-scale (τ). BCPA uses maximum likelihood estimation to fit models with the data segmented at different points, selecting models, and thus significant change points, based on Bayesian Information Criterion (BIC) comparison. Analyzing the tapir's velocity persistence together with the behavioral phases determined by the flat BCPA allowed us to elucidate and interpret patterns in the movement changes (Gurarie et al., 2015). For this analysis the complete track was used (7 months) with velocity persistence (eq. 1) as a movement parameter, and a window size of 36 (equivalent to 1 day approx.). Model requirements were verified prior to the realization of the analysis.

Velocity persistence.

$$Vest(ti) = V(ti)\cos(\Psi(ti)) \tag{1}$$

2.3.3. Utilization distribution estimation (UD) with a dynamic Brownian bridge movement model (dBBMM):

The movement of animals does not coincide with a single unique pattern, but is composed by different movement patterns in response to a determined behavior or action. In this way, the movement varies during day and night, and across months and years (Kranstauber et al., 2012). In this sense, movement models with dynamic Brownian bridges (dBBMM) allow behavioral inference along trajectories (Kranstauber et al., 2014), from movement variance estimates made separately for different times or use zones (Kranstauber et al., 2012), contributing to an approximation of behavioral changes through the trajectories and the spatial use. In accordance with the exploratory analysis and the BCPA results, we used the dBBMM for the two periods of highest contrast: from August to mid-October and from mid-October to February. Both models were run using a window size of 36 (1 day approx.) and margin of 12. The dBBMM is able to account for location errors (Kranstauber et al., 2012), so these were incorporated into the analysis using the error estimates transmitted from the GPS device.
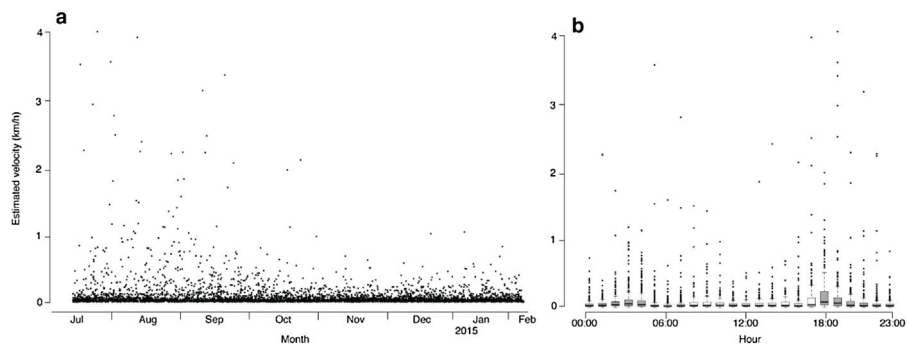
Fig. 2. Estimated daily velocity during the assessment period (a) and daily variability of estimate velocity for the individual steps (b).
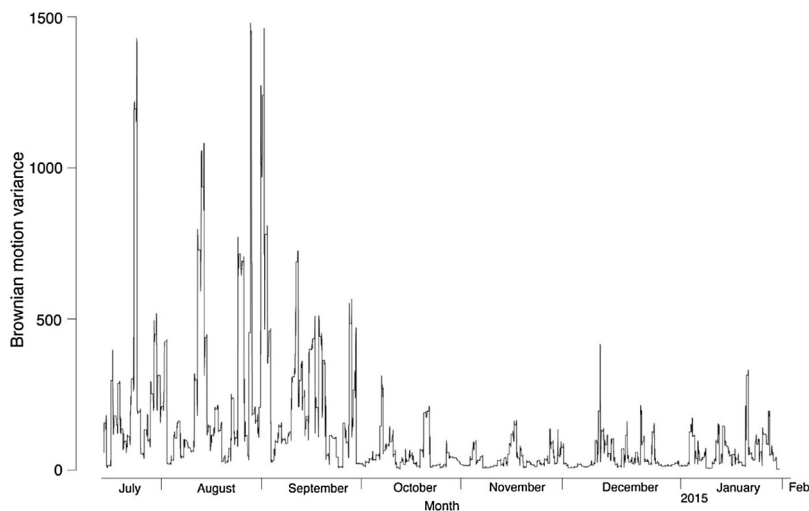

Fig. 3. Brownian motion variance during the assessment period.

3. Results

The individual velocity had a higher variability during the first months of the assessment (from July to October) with maximum values of 4.26 kmh^{-1}. After October, the tapir's movements were slower, with a velocity less than 1.02 kmh^{-1} (Fig. 2a.). Analysis of the variability showed that the tapir's movement was slower from 10:00 to 15:00, and within this time period, the lowest activity was registered from 12:00 to 14:00. On the other hand, the fastest movements occurred during the rest of the day, with activity peaks between 17:00 and 20:00 and between 2:00 and 4:00 (max = 4.26 kmh^{-1}, median = 0.03 kmh^{-1}, Fig. 2b).

Consistent with the velocity analysis for the whole track, the tapir's movement tended to be more tortuous and variable from July to October (Fig. 3, mean = 181.27, max = 1472.51). The largest number of peaks during this period was determined by changes from short to large movements. In this assessment, the individual's mean step distance was 86 m, which is large considering that the mean of short distance displacements was 0.2 m. These large displacements disappeared after mid-October, a time period with low Brownian variance (mean = 35.85, max = 405.82) and individual movements were characterized by short and regular displacements (Fig. 3).

The flat BCPA divided the complete track into 40 change phases. According to the phase number by time period it was possible to define two different stages of change along the complete track: at the first stage (from July to October 21, with 29 phases) was characterized by (i) a higher number of phases, which represent rapid and highly correlated movements matching the large dis-

placements among the resources zones, and (ii) low autocorrelated data and moderate velocity. The several short phases (2–4 days) in this track stage represent constant changes in the individual movement, which could involve a short stay followed by large displacements (Fig. 4). The second stage (From October 21 to February, with 11 phases) was characterized by a low velocity persistence and moderate data autocorrelation. The velocity persistence, variance and time scale decreased (median $\mu = 7.02 \times 10^{-5}$, median $\sigma = 7 \times 10^{-4}$, median $\tau = 0.267$) with respect to the first stage (median $\mu = 1.6 \times 10^{-4}$, median $\sigma = 0.0012$, median $\tau = 0.385$). This overall decrease, coupled with the phases at the second stage (Fig. 4), suggest that the individual had an explorative behavior within the territory and occasional movements along known routes – as was observed from the end of December to January.

From the dBBMM, a relative probability surface is obtained, reflecting variation of space use. Two models were generated to analyze the periods identified by the BCPA, allowing a description of the individual's use of space. In respect to the utilization distribution (UD), the higher probabilities were concentrated at resources sites (palm stands and natural salt licks) from July to October. This is the period during which the tapir spanned wide distances, wandering among feeding sites (palm stands at the north of the study area) and the natural salt lick (located in the south of the study area), and following the same paths repeatedly (Fig. 5). On the other hand, from the end of October to February the tapir's movement was characterized by short displacements and a low utilization of palm stands and natural salt licks (Fig. 5b).
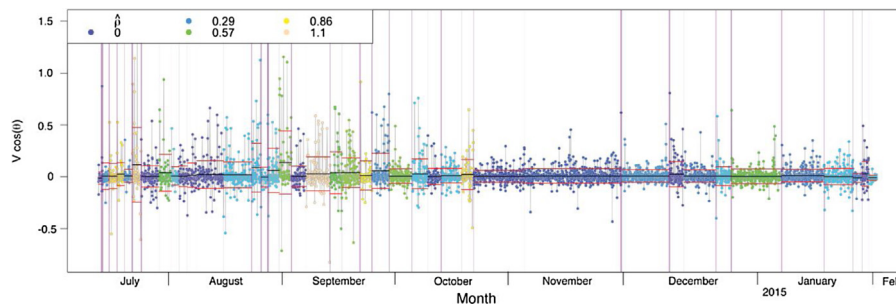
Fig. 4. Results of flat behavioral change point analysis (BCPA). Vertical lines indicate change point and the spaces between these lines are considered phases. The black horizontal lines show the median estimate for each phase, and the red horizontal lines show standard deviation estimates. The colors of the points and vertical lines reflect autocorrelation, with darker colors like blue and purple indicating a lower autocorrelation, and brighter colors like yellow and green indicating higher autocorrelation. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)
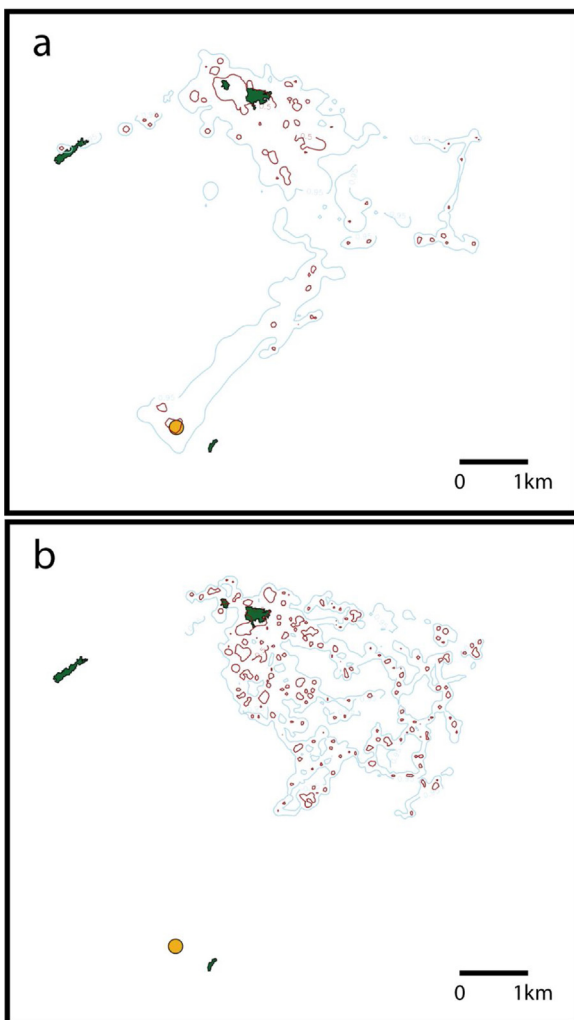

Fig. 5. Estimate of tapirís Utilization Density (UD) for the two stages: July–October (a) and October–February (b). Red lines indicate 5% contour and blue lines 95% contours. Palm stands are in green and natural salt licks in yellow. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

4. Discussion

The results show the complexity of animal movement. This lowland tapir individual exhibited exploratory and food search behavior, both statistically different in terms of estimated velocity variation, Brownian movement variance and BCPA analysis. This was also observed in two different movement phases; the first phase was associated with large movement and a selective use of recourses and it was synchronized with the fructification period of the palm *Mauritia flexuosa*. The second phase was characterized by short displacements and a notable decrease in resources zones and paths. Likewise, the spatial usage of the individual was clearly related with resource availability (mainly of palm stands and natural salt licks), showing that the tapir tended to use the same paths to make trips, similar to what has been reported in the literature (Bodmer, 1990; Medici, 2010).

Palm stands and natural salt licks are sites where herbivorous animals of different species find fruits and nutrients and where animals develop a geophagy or a mating behavior (Molina et al., 2014; Montenegro, 1998; Mueller et al., 2011). The results, displayed at a short temporal scale, meaning a fine scale that show the data structure, show that this individual tapir presented the slowest activity peaks during the day, and the highest activity peaks at night and in the morning linked to nocturnal visits to palm stands and the natural salt licks. This is consistent with other reports of tapirs as animals with mainly night-dusk and cryptic behavior (Blake et al., 2011; Oliveira-Santos et al., 2010). The movement analysis shows that the daytime activity of our tapir is similar to that reported for *Tapirus pinchaque* (mountain tapir) (Blake et al., 2011). This is a remarkable insight given the behavioral differences between these two species.

Similarly, to daily patterns, monthly patterns tended to be linked to the presence of resource sites. Our results show that, for the studied individual, space usage responded to large displacements along known paths between the natural salt licks and the palm stands. This is not a surprise since it is known that tapirs can travel long distances inside the forest to reach natural salt licks (Tobler et al., 2009). The influence of resource sites in the tapir's movement behavior was particularly evident between July and October. During this period, the individual exhibited a faster and more variable movement, likely related to travel and food search. Indeed, it has been suggested that lowland tapirs inhabiting highly conserved forest regions do not use habitats uniformly but make a selective usage of some landscape elements (Daniel and Brooks, 1997). Our results provide evidence of this selection since the individual displayed a clear pattern of movement between food sources like palm stands and salt licks. It also showed a high correspondence between the use of natural salt licks and the fructification period of *M. flexuosa*. This might be due to the low sodium concentrations in the fruits consumed by the tapirs, leading to a need for supplementation through geophagy (Montenegro, 2004) or for detoxification of plant secondary compounds (Blake et al., 2011). This explanation would be consistent with information reported by Vélez Gómez (2015) that in the periods when tapirs do not frequent palm stands, the fiber percentage in their diets increases, providing the sodium concentrations needed.

After October, the individual spent less time at palm stands and did not visit the natural salt licks. Its movements were slower, with short displacements and moderate autocorrelation probably associated with quick and active searches (Gurarie et al., 2015, 2009). This pattern could imply an "explorative" behavior since the directional consistency and velocity persistence suggest that animals walk further from the feeding sites without feeding (Owen-Smith et al., 2010). This explorative behavior could be a response to a synergy effect of seasonal changes in weather (rain period), resource availability and diet (Blake et al., 2011; Vélez Gómez, 2015). During the time the tapir does not use the palm stands, the decrease in the use of natural salt licks is likely because the individual changed its diet and consumed more plant species (Vélez Gómez, 2015). Also, according to the location data distribution and the applied analysis, the movements were erratic and directionless, which can be associated with habitat exploration behaviors.

Large displacements by herbivores are not very common but they can be explained by two main hypotheses (Fryxell et al., 2008): First, large individuals are attracted by exclusive habitat that serve as feeding, mating or refuges, and second, they tend to return to places frequently visited where they can have certainty of finding these resources in a secure manner. In our study, both explanations could apply since large and routine movements were made towards places where fruit and minerals were available. In this sense, palm stands and natural time availability of salt licks are limiting resources that constrain the movement behavior and spatial distribution of tapirs in tropical forests. The difference in the salt lick visit periods might by related with the tapir's physiological requirements and not to its availability variation, e.g. the consumption of the palm fruits may carry stomach illnesses or nutrient deficiency. Also, according to local indigenous knowledge, tapirs use the natural salt lick during the complete year, even in the flooding season, since this species can dive and consume the minerals found in the salt licks under water. Since we already had information on the tapir's location, natural salt licks and palms stands, we are certain that most of the available resources were considered. Other researchers have reported that resource availability is the most important explanatory variable of ungulates' large displacements (Bolger et al., 2008; Teitelbaum et al., 2015).

5. Conclusions

By using GPS telemetry, we were able to compile and analyze a large and unique data set, providing important insights on the movement behavior of a lowland tapir. The GPS approach was not without challenges. Capturing the individual tapir at the study area in order to attach the GPS collar was a complex and arduous task, particularly given the environmental conditions of the northwestern Amazonian zone and the tapir's movement. Collar and satellite equipment, as well as vet services and field work were all costly. However, the data obtained was well worth these challenges. The size of the data set is enormous (a total of 5199 location points) when compared with the data from other studies done in the tropical zone of South America (Castellanos 2013, for instance, reports a set of 350 location points for a similar time period). This allows for analysis at much finer resolutions of space and time.

We found the existence of different behaviors (e.g. exploration and foraging) which were statistically distinguishable and likely associated with diet requirements but possibly also influenced by the individual's experience and memory. Regardless of its underlying explanation, knowledge of this behavior is key to understanding what motivates an animal to move through the landscape. Future research should focus on minimal movement distances, since this parameter that we did not calculate might represent crucial information for population dynamics and habitat conservation. This type of research can be of great use in identifying movement corridors, which can support the development of management plans or connectivity maintenance and the re-establishment of this species (Lédée et al., 2015). Our findings may be a first step towards further understanding ecological processes, such as demography and dispersal, and can provide information to design effective conservation strategies in order to face the growing human threats in the Amazon.

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