Edentata 16 (2015): **46–56**
Electronic version: ISSN 1852-9208
Print version: ISSN 1413-4411
http://www.xenarthrans.org

Spatial distribution, resource use, and behavior of brown-throated sloths (*Bradypus variegatus*) in a multi-use landscape

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Abstract We assessed the spatial distribution, resource use, and activity patterns of brown-throated sloths (*Bradypus variegatus*) in a multi-use landscape in north central Costa Rica. Sloth surveys were conducted during May to August 2014 in two countryside habitats: tree plantations and mixed-use areas. A total of 38 individual brown-throated sloths were detected throughout the study area. Within countryside habitats, brown-throated sloths were more abundant in mixed-use areas (1.2 sloths/km) than in plantations (0.2 sloths/km). Spatial distribution maps and cluster analysis indicated two statistically significant hot spots and one statistically significant cold spot of brown-throated sloths. Sloths were observed on trees with heights ranging from 5.5 to 31.5 m, and were generally found using the upper strata of trees. Thirteen plant species were utilized by brown-throated sloths, with the most common being *Cecropia obtusifolia* (61%), *C. insignis* (7.3%), and *Cordia alliodora* (7.3%). Plants used by sloths for food included *C. obtusifolia, C. insignis*, *Stryphnodendron microstachyum*, and *Tetracera hydrophila.* Sloths spent most of the time resting (48.2%), followed by surveillance (17.3%), feeding (12.6%), grooming (12.2%), and moving (7.2%). While a greater variety of plant species were utilized for resting and surveillance, brown-throated sloths appeared to specialize on fewer species for feeding. The Costa Rican countryside could offer more suitable habitats for brown-throated sloths by incorporating more tree species that sloths use for foraging, such as *Cecropia* spp. Countryside habitats, particularly mixed-use areas, have the potential to provide valuable resources for brown-throated sloths and complement protected areas in the conservation of this species.

Keywords: Costa Rica, countryside biogeography, spatial ecology, three-toed sloth, tropics, Xenarthra

Distribución espacial, uso de recursos y comportamiento de perezosos de tres dedos (*Bradypus variegatus*) en un paisaje de multiuso

Resumen Investigamos la distribución espacial, uso de recursos y patrones de actividad de perezosos (*Bradypus variegatus*) en un paisaje de multiuso de Costa Rica. Durante mayo hasta agosto 2014 llevamos a cabo muestreos de perezosos en dos hábitats rurales: plantaciones de árboles y áreas de uso mixto. En total observamos 38 perezosos y encontramos que fueron más abundantes en áreas de uso mixto (1,2 perezosos/km) que en plantaciones (0,2 perezosos/km). El análisis espacial indicó dos áreas de alto nivel de agrupamiento y un área de bajo nivel de agrupamiento. Los perezosos fueron observados en árboles con alturas entre 5,5 y 31,5 m y se encontraban usando la parte superior del estrato arbóreo. Los perezosos utilizan 13 especies de plantas, siendo las más comunes *Cecropia obtusifolia* (61%), *C. insignis* (7,3%) y *Cordia alliodora* (7,3%). Las plantas que usan como alimento incluyen *C. obtusifolia*, *C. insignis*, *Stryphnodendron microstachyum* y *Tetracera hydrophila*. Los perezosos pasan la mayor parte del tiempo descansando (48,2%), seguido de las siguientes actividades: vigilancia (17,3%), alimentándose (12.6%), acicalamiento (12,2%) y desplazándose (7,2%). Mientras que un variedad de especies de plantas se utilizaron para descanso y vigilancia, los perezosos parecen especializarse en pocas especies para alimentarse. Las zonas rurales de Costa Rica podrían ofrecer hábitats más adecuados mediante la incorporación de más especies de árboles que los perezosos utilizan para alimentación, como *Cecropia* spp. Hábitats rurales, particularmente áreas de uso mixto, tienen el potencial que proveer recursos valiosos para perezosos y complementar las áreas protegidas para la conservación de esta especie.

***Palabras clave*:** Biogeografía de campo, Costa Rica, ecología espacial, perezoso de tres dedos, trópicos, Xenarthra

Introduction

Brown-throated three-toed sloths (*Bradypus variegatus*) are mid-sized, arboreal mammals associated with Neotropical forests, where they rely on the upper levels of the forest canopy to live, feed, and reproduce (Eisenberg, 1989). As a consequence of the poor nutritional quality of their folivorous diet and their extremely low basal metabolic rates, sloths require slow movements and extended periods of inactivity (Montgomery & Sunquist, 1975; Nagy & Montgomery, 1980; Gilmore *et al.*, 2001). These physiological constraints combined with their high reliance on forest cover inhibit sloths from traversing wide gaps in the canopy and dispersing long distances. This weak dispersal ability makes sloths especially susceptible to forest fragmentation and degradation caused by land use change (Tilman *et al.*, 1997). In eastern Nicaragua, for example, fragmentation of the native forest has adversely affected three-toed sloth populations and, in some cases, caused extinction of local populations (Genoways & Timm, 2003).

Brown-throated sloths occur from southern Honduras to southern Brazil and are common inhabitants of primary and secondary forests (Eisenberg, 1989; Emmons & Feer, 1997; Superina *et al.*, 2010). Studies on the home range of adult brown-throated sloths are somewhat variable in their findings, but all available estimates are relatively smaller than expected for a medium-sized mammal. One study on Barro Colorado Island in Panama found the average home range size for *B. variegatus* to be 1.6 ha (Sunquist & Montgomery, 1973). Vaughan *et al.* (2007) estimated that brown-throated sloths in Limón, Costa Rica possessed a median home range size of approximately 5.2 ha. Within their relatively restricted home range, brown-throated sloths travel small distances on a daily basis (<38 m/day in 89% of cases) and typically remain in the same tree for consecutive days before moving to a new tree through the pathways of the canopy (Sunquist & Montgomery, 1973; Montgomery, 1983; Vaughan *et al.*, 2007).

Notably, brown-throated sloths are not entirely dependent on forests to fulfill their resource requirements. Brown-throated sloths have also been observed using other habitats, specifically riparian areas, cacao agroforests, and pastures containing living fencerows and remnant trees (Vaughan *et al.*, 2007; Ramirez *et al.*, 2011). These countryside habitats (Daily *et al.*, 2001) can increase structural complexity and enhance the connectivity of habitats in human-modified landscapes, and therefore provide suitable habitats, resources, and dispersal pathways for a significant portion of the native biota (Harvey *et al.*, 2006; Brockerhoff *et al.*, 2008; Haslem & Bennett, 2008). Whether brown-throated sloths are able to support a self-sustaining population in countryside habitats remains uncertain. Given their low vagility, brown-throated sloths may require supplementation from source populations in neighboring forest patches to maintain a stable population within countryside habitats (Peery & Pauli, 2014).

As human population, food consumption, and the demand for forest products continue to rise over the next century, the pressures of land use change on biodiversity are projected to intensify (Sala *et al.*, 2000; DeFries *et al.*, 2005). All else being equal, species with poor dispersal ability might be disproportionately vulnerable to habitat loss and fragmentation (Kotiaho *et al.*, 2005; Stork *et al.*, 2009). Because sloths are sedentary and highly cryptic animals, making inferences about their habitat associations is often difficult. While a handful of ecological studies have focused on the spatial ecology of sloths in human-dominated landscapes, specifically within shade-grown cacao agroforests (Vaughan *et al.*, 2007; Peery & Pauli, 2014), no research has examined the extent to which sloths use tree plantations or mixed-use areas (*i.e.*, areas containing multiple land uses, such as residential, small-scale agriculture, and secondary forest fragments). Advancing our understanding about how and to what degree sloths use countryside habitats is an important step in assessing and mitigating the effects of land use change on species of low vagility.

The principal objectives of this study were to investigate the spatial distribution, resource use, and activity patterns of brown-throated sloths in a multiple-use landscape in Costa Rica, with specific focus on their use of tree plantations and mixed-use areas.

Materials and Methods

Study area

This study was carried out in San Juan de Peñas Blancas, San Ramón, Costa Rica (10º23'N, 84º37'W) located about 75 km northwest of the capital city of San José (**Fig. 1**). San Juan de Peñas Blancas is located on the Caribbean slope of the Tilarán Mountains, adjacent to the Bosque Eterno de los Niños and the Monteverde Cloud Forest Reserve. This region is classified as tropical premontane wet forest (Holdridge, 1967) with an elevation gradient of 275–465 m above sea level. The mean annual temperature of this region is 24 °C and the mean annual precipitation is approximately 4,500 mm. Mean monthly precipitation varies from 154 mm in February to 540 mm in November, with the majority of the rainfall occurring during June through December.

The study area covers approximately 4 km^2 and is composed of a mosaic of forest and human-modified habitats. The landscape is primarily comprised of forests (59.5%) in different successional stages, specifically secondary forests (45.5%), primary forests (11%), and riparian forests (3%). The next dominant land uses are pastures and small-scale monocultures, which cover 19% and 10% of the landscape, respectively. Two types of countryside habitats, tree plantations and mixed-use areas, are present in the study region. Tree plantations encompass approximately 3.5% of the landscape. Most plantations in the study area are relatively well established (≥ 8 years old), possess a cleared understory, and contain a polyculture of native (*e.g.*, *Astronium graveolens*) and non-native species (*e.g.*, *Tectona grandis* and *Gmelina arborea*). Mixed-use areas comprise a smaller portion of the landscape (~1%), but are often adjacent to pastures and agricultural lands, and thus may be important refuge habitats for biodiversity. Residential areas, unpaved roads, and water cover the remaining 7% of the study area.

Data collection

Sloth surveys. Line transects are a practical and effective method for obtaining qualitative data on the distribution of sedentary organisms, which can then be compared across sites (Anderson *et al.*, 1979). In this study, line transects were used to collect information on the distribution and relative abundances of brown-throated sloths in different countryside habitats. The study region was stratified according to land use type and seven survey sites were selected, four of which were tree plantation sites and three were mixed-use sites (**Fig. 1**).

Within plantation sites, transects were established using a systematic design of parallel transects to ensure equal coverage of the site, and a random first start to provide an element of randomization. Transects were established at least 15 m from surrounding habitats to minimize edge effects. In mixed-use areas, transects were walked along preexisting trails distributed throughout the entire sampling area. Riparian areas were also sampled, but harsh terrain prohibited the inclusion of transects in such sites. Therefore, any observations of brown-throated sloths in riparian areas or forest fragments were performed from unpaved roads, *ad libitum*.

Multiple methods were used to improve detection probability: 1) extensive transect lengths guaranteed adequate coverage of each site; 2) repeated surveys ensured exhaustive sampling; and 3) high powered binoculars (Nikon Monarch 7 – 8x42, Tokyo, Japan) assisted in locating sloths in the canopy. Since species with small area requirements, like the brown-throated sloth, are more prone to regularly use their entire home range for foraging, we expected that sloths would be observed at a constant probability along the sampling effort (de Thoisy *et al.*, 2008).

All transects were walked at a rate of 0.5 km/h during peak sloth activity periods (08:00–16:00 hr; Urbani & Bosque, 2007; Voirin *et al.*, 2014), and brief

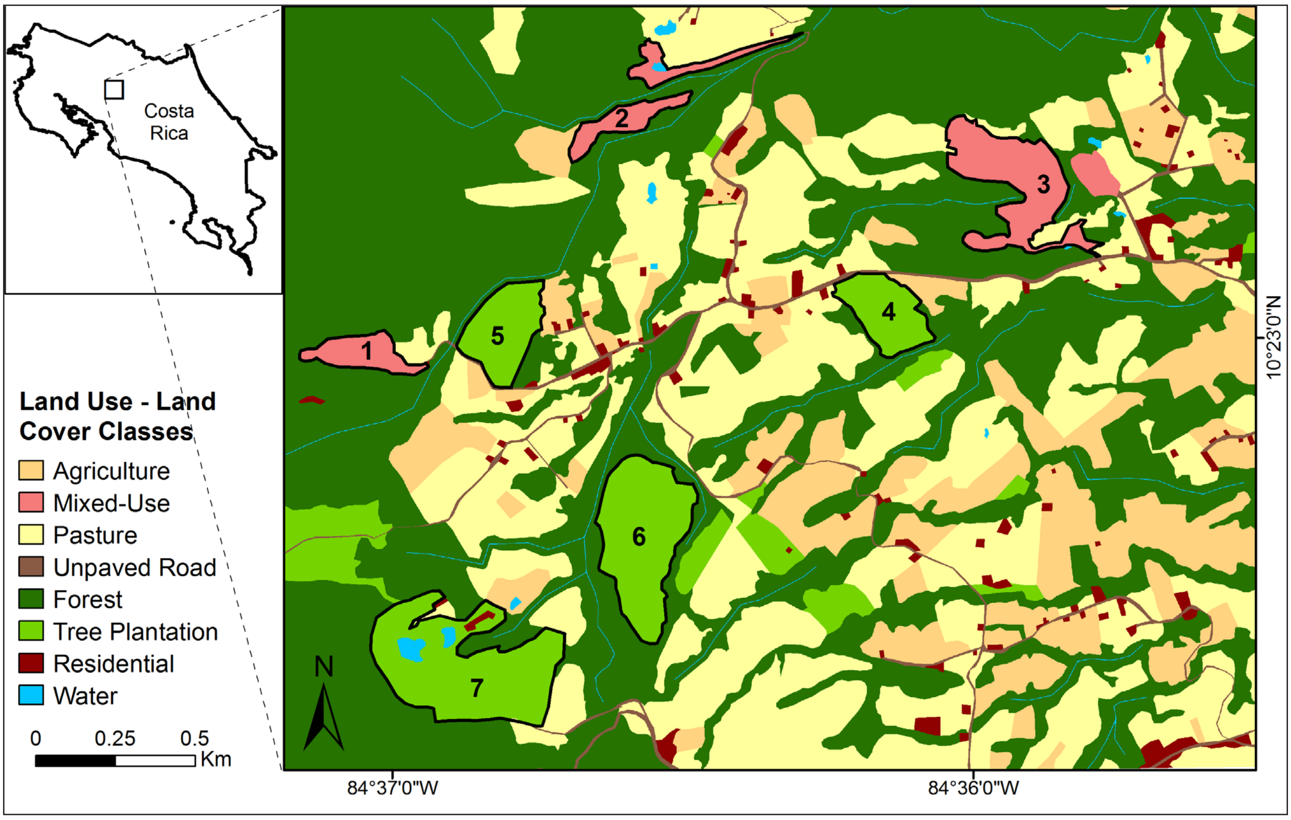

Figure 1. Map of the study region and locations of study sites sampled by line-transects in San Juan de Peñas Blancas, Costa Rica (10º23'N, 84º37'W). Study sites (1–7) correspond with site codes in **Table 1**.

stops were made regularly to scan for sloths with binoculars. To avoid a potential bias in the ability to detect sloths, all transects were walked alone by the same experienced observer (KDN). Surveys were not carried out during periods of heavy rainfall because of the extremely low detectability rates during these conditions. The total sampling effort was 18.7 km (6.2±3.9 km) in three mixed-use areas and 26.5 km (6.6±2.3 km) in four tree plantations, however the sampling effort per unit area was relatively consistent across sites (**Table 1**). On average, there was a slightly lower sampling effort per unit area in plantations because the cleared understories and lower structural complexity improved observer visibility in these areas.

When a sloth was encountered, a photograph was taken using a Canon EOS Rebel T3 digital SLR camera with a 200 mm telephoto zoom lens (Canon USA, Melville, NY, USA). All photographs were catalogued into a library that was used to determine whether each observation was a new individual or a resight, based on marked differences in the sloths' pelage. Sexually mature male brown-throated sloths possess a dorsal speculum that is unique in brightness, shape, and pattern, allowing for the recognition of a particular individual (**Fig. 2**). The lack of a speculum in female sloths makes individual identification slightly more challenging; however, the use of photographs of distinct pelage patterns combined with the time and geographic location of each observation allowed for conclusive identification of individuals. Data presented on sloths are therefore counts and not estimates.

A unique identification number was assigned to each new individual, and GPS coordinates were taken at the base of the tree in which the sloth was located using a Garmin eTrex 20 receiver (Garmin Ltd., Kansas, USA). If the base of the tree was not accessible, the distance from the observer to the tree was measured to the nearest meter using a laser rangefinder (Nikon Aculon 6x20, Tokyo, Japan), and a compass bearing was recorded to the nearest degree. This information was used along with a geographic information system (ArcGIS 10.2; ESRI, 2014) to determine the precise location of the sloth. Tree height and the height of the sloth above ground were calculated using a clinometer to determine which height of the tree was most commonly used by sloths in the study. In addition, all trees utilized by sloths were identified to the species level.

Focal-animal sampling (Altmann, 1974) was used to record brown-throated sloth behavior. The following behavior categories were selected following an ethogram adapted from Urbani & Bosque (2007): 1) feeding; 2) grooming; 3) locomotion; 4) resting; and 5) surveillance. The frequencies and

Figure 2. The speculums of mature male brown-throated sloths are unique for each individual. Speculums differ in brightness, shape, and pattern, and can be used for identification purposes.

Table 1. Characteristics of sampling sites and sampling effort for brown-throated sloth surveys in San Juan de Peñas Blancas, Costa Rica during May–August 2014.

Habitat type	Site	Area (ha)	Total sampling effort (km)	Effort/area (km/ha)	Mean effort/area (km/ha)
Mixed-use	1	2.9	3.9	1.3	1.1
	2	4.5	4.0	0.9	
	3	9.0	10.8	1.2	
Tree plantation	4	4.9	4.5	0.9	0.8
	5	5.6	4.9	0.9	
	6	11.6	8.1	0.7	
	7	15.7	9.0	0.6	

durations of behaviors were continuously recorded for 60 min or until the individual was no longer visible. Each sloth was categorized as either an adult or juvenile/infant based on general body size, and male or female based on secondary dimorphic markings (Emmons & Feer, 1997).

Spatial distribution and clustering. Merely plotting brown-throated sloth localities on a map does not provide sufficient information about distribution patterns. We used two spatial-analysis tools to visualize and quantify spatial patterns in the brown-throated sloth occurrence data. First, we created a heat map using the Point Density tool in the Spatial Analyst toolbox of ArcGIS 10.2 (ESRI, Redlands, CA, USA) to visualize areas of high and low frequency of sloth occurrence. We used a grain size of 0.5 m^2 and a neighborhood of 5 ha to represent the brown-throated sloths' approximate home range. Subsequently, we conducted an optimized hot spot analysis to quantify the observed spatial patterns and identify statistically significant hot and cold spots. A hot spot map was created using the Optimized Hot Spot Analysis tool in the Spatial Statistics toolbox of ArcGIS 10.2. Optimized hot spot analysis aggregates incident points into fishnet (grid-like) polygons and uses the Getis-Ord Gi* statistic (Getis & Ord, 1992) to determine areas of statistically significant spatial clustering. The Optimized Hot Spot Analysis tool selects an optimal scale of analysis by assessing the intensity of clustering at increasing distances, and applies a false discovery rate correction when determining statistical significance to correct for multiple testing and spatial dependence. The resulting z-scores indicate whether the observed spatial clustering is more or less pronounced than expected by random. Statistically significant positive z-scores indicate high concentration areas (hot spots) and statistically significant negative z-scores indicate low concentration areas (cold spots).

Results

Use of countryside habitats

A total of 38 brown-throated sloths were encountered throughout the study area during May–August 2014 (**Fig. 3**). Twenty-seven sloths were observed from transects in tree plantations and mixed-used areas. A greater number of sloths was detected within mixed-use areas (1.2 sloths/km) than in plantations (0.2 sloths/km), despite similar survey effort per unit area. Sloths were also detected in riparian forest and secondary forest fragments from unpaved roads between survey sites, however survey effort was much lower in these habitat types because they were not the primary focus of the study.

The observed sex ratio was 1.7:1 (male:female), comprising 58% males (n=22), 34% females (n=13), and 8% juvenile/infant sloths (n=3). On four separate occasions, one male and one female were observed together in the same tree for several days, although copulation was never observed. Twenty-five individuals were resighted at least once (*i.e.*, identified by distinct patterns in their pelage, as well as time and location of last observation), generally in the same tree or within 50 m of the original sighting.

Use of floristic resources

The utilization of plant species by brown-throated sloths is presented in **Table 2**. Brown-throated sloths were observed using a total of 41 plants belonging to 13 species during the four months of this study. Brown-throated sloths were predominantly detected on *C. obtusifolia* (61%), followed by *C. insignis* (7.3%), and *Cordia alliodora* (7.3%). Both *Cecropia* species were most often used for feeding, although brown-throated sloths were also observed feeding on *Stryphnodendron microstachyum* and a liana species, *Tetracera hydrophila*, on one occasion. It is worthy to note that we recorded only a single incident of a sloth using a plantation tree (*Terminalia oblonga*). All other detections in tree plantations were of sloths using *C. obtusifolia* and *Pourouma bicolor* (Family: Urticaceae).

Trees utilized by brown-throated sloths ranged from 5.5 m in *C. obtusifolia* to 31.5 m in *C. insignis*, with an average of 20.9±0.9 m for all tree species. Aside from one instance of a juvenile sloth on a *C. obtusifolia* measuring 5.5 m, sloths were not observed using trees less than 10 m. On average, sloths were situated 16.2±0.8 m above the ground. The average relative position of sloths in trees was 0.78, with 0 representing the ground level and 1 representing the tree crown. On several occasions, a sloth was observed climbing up the lower portion of the tree, but never remained at the base of the tree for more than several seconds.

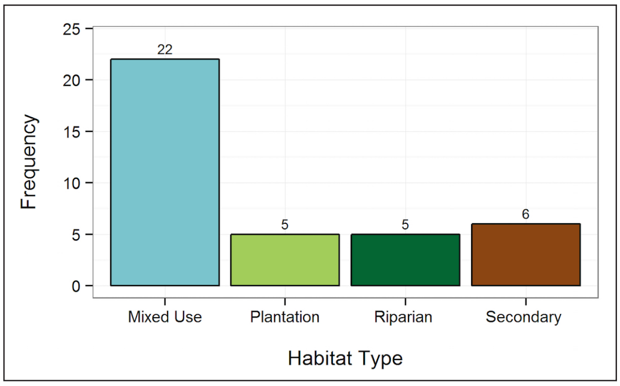

Figure 3. Relative frequency of brown-throated sloth observations in four habitat types throughout San Juan de Peñas Blancas, Costa Rica. Numbers above histograms indicate the number of individuals observed.

Activity patterns

The activities of brown-throated sloths were observed for a total of 49.64 hours (**Table 3**). Of all activities, sloths spent the greatest amount of time resting (48.2%), followed by surveillance (17.3%). Sloths devoted a similar amount of time to feeding (12.6%) and grooming (12.2%), while locomotion accounted for 7.2% of their activities. Brown-throated sloths exhibited differential use of plant species. Throughout the study, brown-throated sloths spent most of their time in *Cecropia* trees (84.8%), especially *C. obtusifolia* (77.3%). *Cecropia* spp. were used by sloths for all activities: feeding, grooming, locomotion, resting, and surveillance. Sloths were observed feeding on four species of plants, however feeding primarily occurred on *Cecropia* spp. (92.2%). Stationary behaviors (*i.e.*, resting and surveillance) took place in a greater diversity of tree species than foraging behaviors.

Spatial distribution and clustering

The heat map revealed two areas of relatively high frequencies of sloth occurrence, represented by the regions in red and orange, as well as many

Table 2. Use of plant species by brown-throated sloths in San Juan de Peñas Blancas, Costa Rica during May–August 2014, including mean (±SEM) height of sloth above ground, mean (±SEM) tree height, and mean relative position of sloth. Relative position of sloth ranges from 0 to 1, with 0 representing the ground level and 1 representing the tree crown.

Plant species	Family	N	Mean height of sloth (m)	Mean tree height (m)	Mean relative position of sloth
Cecropia obtusifolia	Urticaceae	25	15.4±0.9	20.5±1.2	0.75
Cecropia insignis	Urticaceae	3	19.6±5.1	27.2±2.4	0.72
Cordia alliodora	Boraginaceae	3	22.2±1.9	24.1±2.3	0.92
Dendropanax arboreus	Araliaceae	1	11.4	13.6	0.84
Inga coruscans	Fabaceae	1	13.2	17.8	0.74
Ocotea cernua	Lauraceae	1	20.5	21.8	0.94
Pourouma aspera	Urticaceae	1	19.1	22.0	0.87
Stryphnodendron microstachyum	Fabaceae	1	19.6	30.7	0.64
Terminalia oblonga	Combretaceae	1	14.0	21.8	0.64
Tetracera hydrophila	Dilleniaceae	1	19.5	21.0	0.93
Trichospermum grewiifolium	Malvaceae	1	11.3	19.2	0.59
Virola koschnyi	Myristicaceae	1	11.8	12.1	0.98
Vochysia guatemalensis	Vochysiaceae	1	12.5	13.3	0.94
Average			**16.2±0.8**	**20.9±0.9**	**0.78**

Table 3. Extent of time brown-throated sloths utilized 13 plant species for different activities in San Juan de Peñas Blancas, Costa Rica during May–August 2014.

Plant species	All activities Hours (%)	Feeding Hours (%)	Grooming Hours (%)	Locomotion Hours (%)	Resting Hours (%)	Surveillance Hours (%)
Cecropia obtusifolia	38.36 (77.3)	5.42 (84.4)	4.31 (69.2)	2.35 (64.0)	19.11 (77.9)	7.17 (81.6)
Cecropia insignis	3.70 (7.5)	0.50 (7.8)	0.70 (11.2)	0.50 (13.6)	1.62 (6.6)	0.38 (4.3)
Cordia alliodora	2.08 (4.2)	0.00 (0.0)	0.42 (6.7)	0.17 (4.6)	1.16 (4.7)	0.34 (3.9)
Dendropanax arboreus	0.75 (1.5)	0.00 (0.0)	0.20 (3.2)	0.20 (5.4)	0.00 (0.0)	0.35 (4.0)
Inga coruscans	1.50 (3.0)	0.00 (0.0)	0.35 (5.6)	0.10 (2.7)	0.90 (3.7)	0.15 (1.7)
Ocotea cernua	0.25 (0.5)	0.00 (0.0)	0.00 (0.0)	0.10 (2.7)	0.00 (0.0)	0.15 (1.7)
Pourouma aspera	0.50 (1.0)	0.00 (0.0)	0.25 (4.0)	0.10 (2.7)	0.00 (0.0)	0.15 (1.7)
Stryphnodendron microstachyum	0.50 (1.0)	0.25 (3.9)	0.00 (0.0)	0.15 (4.1)	0.00 (0.0)	0.10 (1.1)
Terminalia oblonga	0.50 (1.0)	0.00 (0.0)	0.00 (0.0)	0.00 (0.0)	0.5 (2.0)	0.00 (0.0)
Tetracera hydrophila	0.25 (0.5)	0.25 (3.9)	0.00 (0.0)	0.00 (0.0)	0.00 (0.0)	0.00 (0.0)
Trichospermum grewiifolium	0.50 (1.0)	0.00 (0.0)	0.00 (0.0)	0.00 (0.0)	0.5 (2.0)	0.00 (0.0)
Virola koschnyi	0.50 (1.0)	0.00 (0.0)	0.00 (0.0)	0.00 (0.0)	0.5 (2.0)	0.00 (0.0)
Vochysia guatemalensis	0.25 (0.5)	0.00 (0.0)	0.00 (0.0)	0.00 (0.0)	0.25 (1.0)	0.00 (0.0)
Total	**49.64 (100)**	**6.42 (12.6)**	**6.23 (12.2)**	**3.67 (7.2)**	**24.54 (48.2)**	**8.79 (17.3)**

areas of relatively low frequencies of occurrence, denoted by the regions in green and blue (**Fig. 4**). Assumptions were not made about the frequency of occurrence at locations where no sloths were observed, or where surveys were not conducted. The optimized hot spot analysis identified statistically significant clustering of brown-throated sloths using an optimal fixed distance band of 401.3 m (**Fig. 5**). Two statistically significant hot spots ($1.7 \leq Z \leq 4.3$) and one statistically significant cold spot ($-2.3 \leq Z \leq -1.7$) were detected.

Discussion

Our results demonstrate that brown-throated sloths in this study appear to be able to adapt to the disturbed and fragmented landscape by utilizing countryside habitats, specifically mixed-use areas and tree plantations. This may be a consequence of the high density of pioneer species that is typical of these early-mid successional habitats. Brown-throated sloths were relatively more abundant in mixed-use areas than in tree plantations. The greater structural complexity of the vegetation and diversity of habitats in mixed-use areas could account for the differential use of these areas, however future studies should aim to quantify the vegetation structure of these sites to confirm this speculation.

Previous studies have found evidence that three-toed sloths favor habitats based on their floristic composition (Urbani & Bosque, 2007; Falconi *et al.*, 2015). Habitats containing high densities of pioneer tree species, specifically *Cecropia* spp., harbor important components of sloths' diets (Vaughan *et al.*, 2007). In our study area, *C. obtusifolia* retains its leaves and continuously flowers throughout the year (Zalamea *et al.*, 2011). The constant supply of young leaves and flowers could explain the high number of observations of sloths in these trees. The use of *Cecropia* spp. by brown-throated sloths in this study is in accordance with other studies on the habitat selection and use of floristic resources by three-toed sloths in Costa Rica (Vaughan *et al.*, 2007; Ramirez *et al.*, 2011; Mendoza *et al.*, 2015). The higher relative density of *Cecropia* spp. in mixed-use areas compared to plantations could be attracting sloths to this land use type. However, it remains unclear whether a combination of vegetation structure together with an abundance of preferred plant species might better explain the differential habitat use by sloths in this study. Interestingly, even though *Cecropia* were sparse in tree plantations, sloths appeared to utilize the few *Cecropia* trees that were present, remained in them for several days before departing, and returned to the same *Cecropia* frequently. This suggests that while sloths do not appear to be regularly using plantation trees for feeding, they may be using

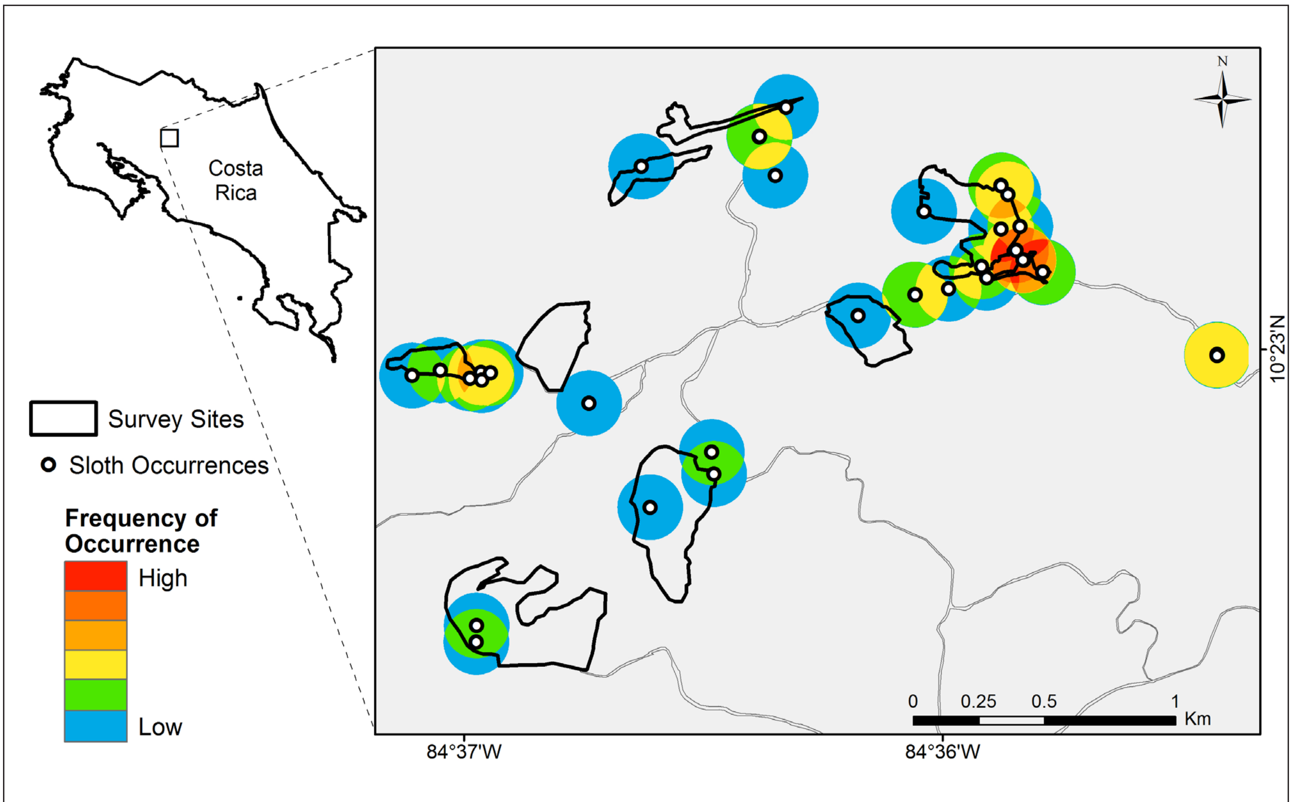

Figure 4. Spatial distribution and relative frequency of occurrence of brown-throated sloths (N=38) in San Juan de Peñas Blancas, Costa Rica during May–August 2014. Areas in red correspond with a high frequency of occurrence, while areas in blue correspond with a low frequency of occurrence.

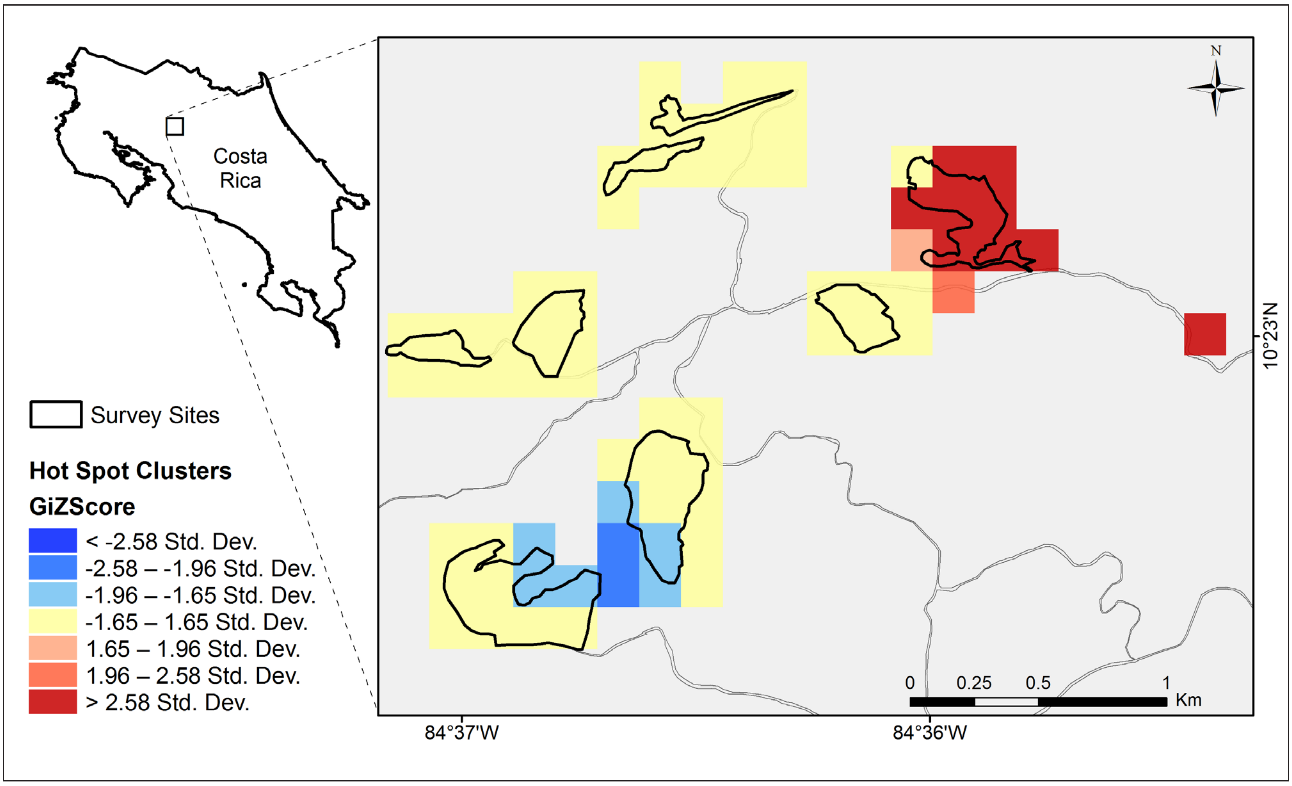

FIGURE 5. Optimized hot spot analysis (Getis-Ord Gi*) of brown-throated sloths (N=38) in San Juan de Peñas Blancas, Costa Rica during May–August 2014. Shades of red indicate significant spatial clusters of high values (hot spots), shades of blue indicate significant spatial clusters of low values (cold spots), and yellow indicates random distribution with no spatial clustering.

them to aid in dispersal to *Cecropia* trees nearby. Plantations could potentially serve as more favorable habitats for brown-throated sloths, and perhaps other species (Medellin, 1994), if they comprised a greater abundance of plants species used for foraging, such as *Cecropia* species.

While the sloths in our study specialized on only a few plant species for feeding, they appeared to be generalists in their use of floristic resources for other activities. These findings are concordant with the behavioral patterns of *Bradypus* sloths in other studies (Queiroz, 1995; Chiarello, 1998; Urbani & Bosque, 2007). Given their documented specialized folivorous diets and low metabolic rates, it is not surprising that our study sloths were observed consuming only four plant species, but utilized a wider range of species for activities that require minimal energy expenditure, such as resting.

Consistent with previous studies, our results indicate that sloths tend to frequent the intermediate and upper portions of the canopy (Queiroz, 1995; Urbani & Bosque, 2007; Castro-Vásquez *et al.*, 2010). One possible explanation for the differential use of the upper strata may be directly related to ambient temperature and weather (Urbani & Bosque, 2007; Giné *et al.*, 2015). Throughout the four months of our study, the region received an above-average amount of precipitation (2287.5 mm, personal observation). Because of their low body temperature and limited thermoregulatory abilities (McNab, 1978), sloths probably took advantage of the upper portions of trees to enhance their exposure to solar radiation, increase core body temperatures, and dry out after periods of rain.

Sloths also respond to cold and cloudy weather by adopting a huddled posture to conserve heat (Urbani & Bosque, 2007; Giné *et al.*, 2015). Perhaps the high proportion of the time sloths were observed resting compared to other activities could be a consequence of the unusually rainy conditions during our study. An opportunity for future research may be to repeat this study in the dry season to investigate the temporal variation of activity patterns by brown-throated sloths in our study area. Seasonal differences in activity patterns have previously been shown for *Bradypus* spp., however they vary by geographic region (Chiarello, 1998; Castro-Vásquez *et al.*, 2010). Given that our study area experiences significantly more rainfall and cooler daytime temperatures during June–December, we expect that sloth activity patterns would also differ across seasons. Moreover, activity levels can depend on the time of day (Urbani & Bosque, 2007), and vary among individuals in a population (Sunquist & Montgomery, 1973; Chiarello, 1998). In this study, surveys started in the morning and ended in the late afternoon. Perhaps nocturnal sampling could also be conducted on sloths to improve our understanding of their activity patterns throughout the 24-h cycle.

The heat map and hot spot analysis collectively revealed information about the spatial patterns of brown-throated sloths in the study area. The heat map identified two regions with high frequencies of sloth occurrence, both of which occurred in mixed-use areas. Of these two areas, only one demonstrated statistically significant clustering of sloths based on the hot spot analysis. Additionally, the hot spot analysis detected a statistically significant clustering of sloths in an area that exhibited only a moderate frequency of occurrence according to the heat map. These results suggest that while heat maps are excellent tools for visualizing the spatial distribution of occurrence data, they may introduce bias when identifying areas of high or low occurrence. The disparity in the two distribution maps is likely related to the difference in neighborhood sizes used in the analyses. The Optimized Hot Spot Analysis tool determines the optimal fixed distance band based on peak clustering, whereas the neighborhood size parameter of the Point Density tool is user-defined, and therefore prone to bias. Care should be taken when defining the extent of the spatial neighborhood, as this may influence the interpretation of the output. When possible, heat maps should be used in combination with statistical analyses, such as optimized hot spot analysis, to properly identify spatial patterns in the data.

In our study area, it appears that mixed-use areas can provide suitable habitat for brown-throated sloths, and one mixed-use site in particular is a significant sloth hot spot. Sloth hot spots can be used in the development of sustainable land management plans that promote sloth occurrence and increase suitable habitat. While the identification of sloth hot spots aids with pinpointing areas that warrant attention from land managers, it does not reveal any information about neighboring land uses, degree of fragmentation, or local habitat structure that may be correlated with the hot spots. Nevertheless, the maps produced in this study provide valuable information on the geographic distribution and spatial clustering of brown-throated sloths in the study region, facilitates visual detection of patterns in the data, and may be used in further analyses, such as quantifying changes in sloth distribution over time.

We believe that because of the cryptic and sedentary nature of brown-throated sloths, this study provides a conservative estimate of the relative use of countryside habitats by sloths. We expect that a greater number of sloths are using tree plantations and mixed-use areas during periods that were not included in our surveys (*e.g.*, night time and dry season), so the potential for these countryside habitats to support a higher abundance of sloths appears promising. It still remains unclear, however, whether brown-throated sloths are able to support a self-sustaining population in these areas. It is possible that because of their limited spatial flexibility, they might require immigration from surrounding forest patches to sustain a stable population (Peery & Pauli, 2014). This is a similar concern among other taxa, including birds and insects (Hughes *et al.*, 2002; Horner-Devine *et al.*, 2003). More detailed population studies are needed to assess the potential for countryside habitats to support populations that are sustainable.

Conservation and management implications

A key management challenge in human-modified landscapes is to maintain a balance between agricultural production and biodiversity conservation. There is no substitute for the habitats, resources, and ecosystem services provided by forests, and thus the preservation of large tracts of intact forest must take precedence in conservation planning. However, the management of countryside habitats should also be a priority because of their potential to maintain and restore biodiversity throughout the Neotropics (Lees & Peres, 2006; Haslem & Bennett, 2008). In integrated landscapes formerly dominated by forest, countryside habitats can complement conservation reserves and protected areas (Daily *et al.*, 2001; Mendenhall *et al.*, 2011). Our study demonstrates the potential value of countryside habitats, especially mixed-use areas, in providing suitable habitat for brown-throated sloths by increasing structural complexity and tree cover compared to cattle pastures and cropland. Hot spot maps provide graphical tools for land managers and local actors that facilitate the visualization of focal areas for conservation efforts. The identification of sloth hot spots may stimulate further research in this region to determine which specific factors are driving the spatial ecology of brown-throated sloths. Future research should focus on assessing how different habitat characteristics influence the occurrence of brown-throated sloths in human-modified landscapes so that conservation efforts can be effectively prioritized.

Acknowledgements

We thank the Soltis Center for Research and Education for logistical support, Pablo Castro for assisting with satellite imagery, and numerous landowners for granting access to their properties. This research was conducted in accordance with the laws of the Costa Rican government (MINAE-SINAC; Resolución N° SINAC-SE-GASP-PI-R-075-2014). Financial support was provided by the Department of Wildlife and Fisheries Sciences, Texas A&M University.

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Received: 22 September 2015; Accepted: 8 December 2015