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Original Paper

Spatial ecology and conservation of two sloth species in a cacao landscape in limón, Costa Rica

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Abstract The spatial ecology of sloths was studied in an agricultural landscape in Limón Province, Costa Rica. Two sloth species, the three-toed sloth (*Bradypus variegatus*) and the two-toed sloth (*Choloepus hoffmanni*), actively used and traveled through a cacao agroforest and its contiguous living fence rows and riparian forests. This agroecosystem was embedded in an agricultural landscape dominated by banana and pineapple plantations and pastures with dispersed trees. The two-toed sloth (*C. hoffmanni*) was found in 101 tree species and used 34 for food; the three-toed sloth (*B. variegatus*) was found in 71 tree species and used 15 for food. Choice of preferred species differed between the two sloth species. Trees commonly used by sloths for food and/or refuge in the cacao agroforest included *Erythrina poeppigiana*, *Cecropia obtusifolia*, *Leucaena leucocephala*; in the living fence rows, *Cordia alliodora*, *Erythrina poeppigiana, Ocotea sinuata* and *Trophis racemosa*; in the riparian forests, *Coussapoa villosa, Cecropia obtusifolia, Hura crepitans, Pterocarpus officinalis* and *Spondias mombin*; and in the pastures with dispersed trees, *Cordia alliodora, Coussapoa villosa*, *Erythrina poeppigiana*, *Ocotea sinuata* and *Hura crepitans*. This study demonstrates the importance of the cacao agroforest as well as arboreal elements in other land uses in providing resources for sloth conservation in a larger agricultural landscape.

Keywords Cacao - *Bradypus variegatus* - *Choloepus hoffmanni* - Dispersed trees - Habitat use - Home range - Living fence rows - Riparian forest - *Theobroma cacao*

Introduction

Agriculture in Central America has been a major factor in land use change, habitat loss and biodiversity reductions (Sánchez-Azofeifa et al. 2001; Helmuth and Lambin 2002). Large scale production of 'estate crops' such as bananas, pineapple and intensively grown coffee simplify landscapes and reduce floral and faunal diversity (Helmuth and Lambin 2002; Tilman et al 2002). Agroforestry practices that integrate trees into agricultural landscapes can help diversify production and secure additional social, economic and environmental benefits including biodiversity and soil conservation (Schroth et al. 2004; Harvey et al. 2005a; McNeely and Schroth 2006). Cacao (*Theobroma cacao*) is commonly grown in agroforestry systems with diversified tree shade, especially in Latin America and parts of Africa. Cacao farms cover extensive areas in tropical Africa (4.9 million ha), America (1.4 million ha), and Southeast Asia (0.7 million ha) (FAO 2004). Cacao agroforests can provide a livelihood for small-scale farmers by providing a diversity of products including cacao beans, timber, fruits, medicinal products, and potentially ecotourism and carbon credits (Ruf and Schroth 2004).

Traditional shade cacao agroforests have been promoted as a means to conserve animal biodiversity (Rice and Greenberg 2000; Waltert et al. 2004; Kessler et al. 2005). However, little is known about how species use these habitats and move within these landscapes. Most research has simply focused on compiling species lists, e.g., of insects (Leston 1970; Roth and Perfecto 1994), birds (Greenberg et al. 2000; Reitsma et al. 2001) and mammals (Guiracocha 2000; Guiracocha et al. 2001) within cacao agroforests, without providing information on how these animals use resources within the agroforestry systems or move within these systems.

Three-toed sloths (*Bradypus variegatus*) and two-toed sloths (*Choloepus hoffmanni*) are among the largest wildlife species observed in Costa Rican cacao farms (Vaughan et al. 2006). They may comprise 25–67% of total vertebrate biomass in some neotropical forests

(Eisenberg and Thorington 1974; Montgomery and Sunquist 1975). Their arboreal, nocturnal and cryptic habits make sloths among the least studied of neotropical mammals. Currently, three-toed sloths are recognized as 'endangered' by the Costa Rican government and the two-toed sloths are listed on CITES "Red Data List" although these listings probably result more from a lack of information than from real endangerment. Few ecological studies have focused on sloth distribution (Wetzel and Avila-Pires 1980; Wetzel 1985; Genoways and Timm 2003) and home range size and habitat use in forested regions (Sunquist and Montgomery 1973; Montgomery and Sunquist 1978; Chiarello 1998; Chiarello et al. 2004). However, no research has addressed sloth use of cacao agroforests or agricultural landscapes.

The objective of this research was to study the spatial ecology (habitat use, preferred tree species use, movement and home range) of two-toed and three-toed sloths in a cacao agroforest and adjacent land uses in Costa Rica. Understanding sloth use of and movement within such landscapes would help in planning sloth (and other biodiversity) conservation strategies and developing scientifically based recommendations for biodiversity friendly management of cocoa and other land use systems.

Materials and methods

Study site

The study area was an agricultural landscape near the village of Pueblo Nuevo de Guácimo, Limón Province, Costa Rica (10°20″ N, 83°20″ W), 85 km northeast of San Jose, the capital city. This area is in the Premontane Wet Forest Life Zone (Holdridge 1964) about 100 meters above sea level. The principal study site was a 120-hectare organic cacao farm (Figs. 1 and 2) surrounded by banana and pineapple monocultures and several cattle ranches. The cacao farm includes a habitat matrix consisting of cacao under shade with riparian forests and living fences surrounding the cacao plantation. The fence rows consist primarily of *Castilla elastica*, *Erythrina poeppigiana*, *Ficus werckleana*, *Spondias mombin* and *Cordia alliodora*. The farm is bisected by several seasonal streams and drainage canals. Nearby pastures are dominated by African star grass (*Cynodon nlemfuensis*) and contain isolated large trees such as *Coussapoa villosa*, *Ocotea sinuata*, *Erythrina poeppigiana* and *Hura crepitans*. The total size of this study landscape for purposes of estimating relative proportions of different land uses was 3,000 hectares. The cacao agroforest appears to function as a corridor connecting Tortuguero National Park to the northwest with fragments of riparian forest on the Rio Jimenez to the southwest.

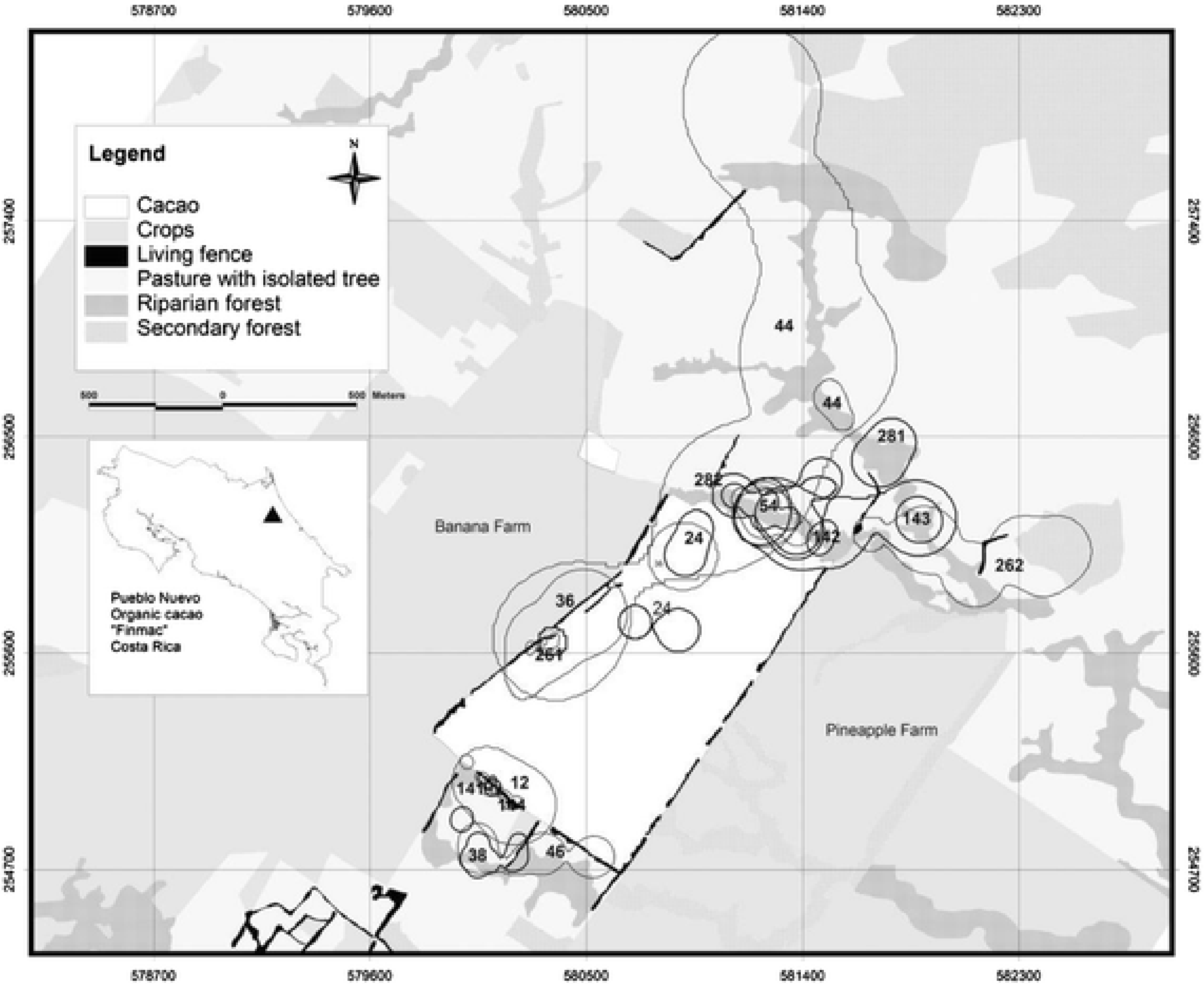

Fig. 1 Home ranges of three-toed sloths estimated by the MCP method, Pueblo Nuevo de Guácimo, Limón, Costa Rica, 2004-2005. The polygons with numbers depict the home ranges of the different marked sloth individuals

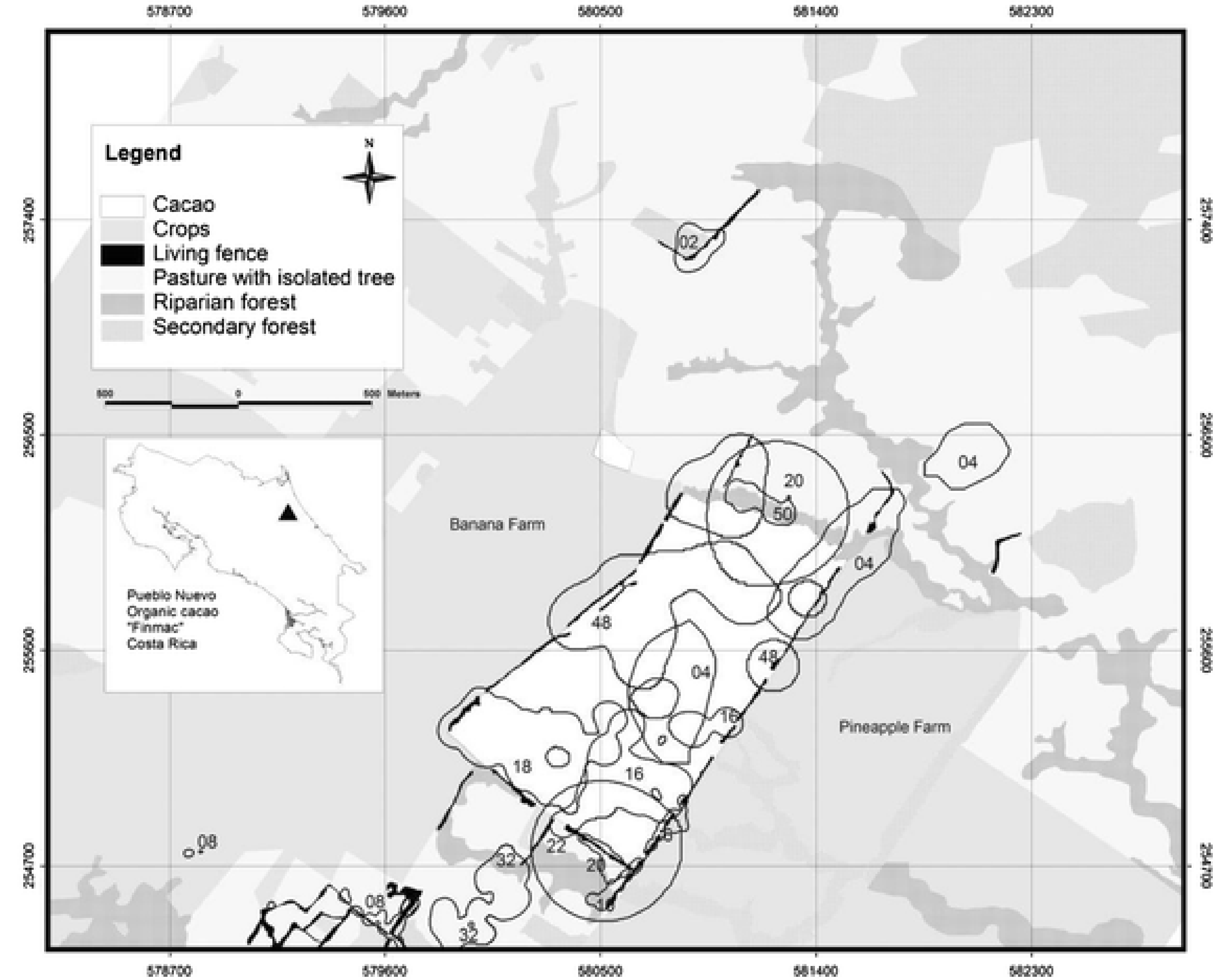

Fig. 2 Home ranges of two-toed sloths estimated by the MCP method, Pueblo Nuevo de Guácimo, Limón, Costa Rica 2004-05. The polygons with numbers depict the home ranges of the different marked sloth individuals

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Data collection

Habitat description and vegetation inventories

The principal vegetation types in the study area, identified in infrared satellite images (Carta 2005 Project, National Program for Aerospace Missions and Remote Sensing), included cacao agroforests, banana and pineapple monocultures, subsistence crops (corn), secondary forest fragments, living fence rows, pasture with isolated trees and riparian forest (Fig. 1). To estimate woody plant diversity and abundance in these vegetation types, we established line transects and circular plots in which we identified trees to species. A total of 7.22 ha was inventoried to assess tree species diversity and the composition of trees in each habitat (Table 2). These inventories included three riparian forest segments (0.2, 0.2 and 0.35 ha), 5 ha of pasture with isolated trees, 0.9 ha of living fence rows, and 0.57 ha of cacao agroforests. We used the line transect method to sample vegetation in living fence rows with 150 m × 5 m transects randomly placed within longer fence rows. Within the riparian forest, a 50 m x 10 m transect was placed perpendicular to the river or stream for each 150 linear meter of forest. Within the cacao farm we used 15 circular plots with a radius of 11 m (0.038 ha) randomly placed using the "random point generator v.1.24" function available from (www.esri.com). Vegetation in the pasture was sampled in five 1 ha circular plots (radius of 57 m) selected by randomly locating plots on a large grid map of the area.

Capture and radio telemetry

Between January 2004 and December 2005, 27 sloths were caught by hand while they rested in trees (Table 1). Most animals were initially caught in the cacao agroforest or adjacent living fence rows because these animals were most accessible and easy to capture. Animals were transported in a burlap sack to a processing site where they were sexed, weighed, measured, and a pit tag (Trovan, Electronic Identification System, ID-100US) was inserted sub-dermally between the shoulder blades. A radio collar (Mod-210; Telonics-Electronics Consultants, 932 E. Impala Avenue, Mesa, Arizona 85204-6699) was placed around each sloth's neck before they were released at their capture site. Sloths were subsequently relocated at three-day intervals beginning in January 2004; relocations were conducted at 4-day intervals starting in January 2005. Each radio-collared animal was located using portable Yagi antennas (RA-2AHS) and TR-4 receivers (Telonics, Mesa, Arizona); once the sloth was visually sighted, geographic coordinates were collected (Magellan Sport Track GPS) beneath each resting individual and the tree species where each animal was found and plant part eaten (if observed) were identified. Rarely are radio telemetry data taken with such accuracy (1 m average) because the researcher typically cannot approach his subject animal.

Table 1 Number of sloth species of each sex fitted with a radio collar, Pueblo Nuevo de Guácimo, January 2004–December 2005)

	Bradypus variegatus	***Choloepus hoffmannii***
Male	7	6

Female	8	6
Total individuals	15	12
Total relocations (# of sightings)	1296	1902

Data analysis

Floristic diversity and composition of different land uses

We used the software "Species Diversity and Richness" (Pisces Conservation Ltd 1998) to estimate several biodiversity indices. We estimated species richness in each sampled habitat (Hellmann and Fowler *1999*), and we used rarefaction analysis to provide a meaningful interpretation of species richness and species evenness among habitats that differed in total number of individuals by calculating an expected number of species (E[Sn]) for a given sample size from each site (James and Rathbun *1981*). To estimate species diversity we calculated a Shannon-Wiener diversity index for each habitat type. We then generated a frequency distribution to describe the structure and composition of each habitat. All habitat evaluations were completed in 2006.

Analysis of home range use

Monthly and annual home range sizes were estimated for each sloth using 95% fixed-kernel home-range areas with least squares cross-validation (Seaman et al. *1999*) using the ArcView 3.3 (Environmental Systems Research Institute, Inc., Redlands, California); the "animal movement" and "home range" extensions were used to estimate home range and to map these estimates onto the landscape for each individual. We determined the proportion of the range that could be defined as 95% contour lines of the fixed-kernel estimation to assess centers of activity per species. All sloths relocations were used for home-range estimation because kernel estimators are robust to violations of independence (Swihart and Slade *1997*).

Habitat use

We used infrared images (Carta 2005 Project, National Program for Aerospace Missions and Remote Sensing) to delineate each habitat type on the landscapes where sloths were located. Global Positioning System (GPS) points were plotted for each relocation of a specific animal in a specific habitat. In addition to providing the data for home range estimates, these relocations also facilitated the estimation of 'potential available habitat.' To establish 'potential available habitats', radio telemetry locations of all animals for each species were mapped onto the landscape and the vegetation cover map was superimposed to generate a set of buffers of 30 m radius using "Xtool" (www.esri.com) of ArcView 3.3. Thirty meters was considered the margin of error for the reading with GPS equipment. The area delineated by this buffer was considered the 'potential available habitat' for each sloth species. The 'potential available habitat' for the two sloth species differs slightly because the home ranges established using telemetry data only partially overlapped (Figs. 1 and 2). The 'expected use' for each habitat type was estimated as the percentage of each habitat type that occurs on the entire landscape (Biotas software, version 1.03.1 Alpha, Ecological Software Solution). The total number of observed animal-location points within a habitat type was compared with that expected if occurrence in any habitat is random using Chi-square goodness-of-fit tests (Neu et al. *1974*; White and Garrott *1990*).

Preferential tree resource use

Relocations of individual sloths in individual trees were recorded by tree species for each habitat type. Estimates of the frequency of occurrence of each tree species were based on vegetation inventories conducted in each habitat type. The frequency of relocations in different trees was compared with the frequency of occurrence of trees in each habitat type using Chi-square goodness of fit tests. Data for the tree species most commonly encountered during telemetry relocations are presented in Table 3. Tree species most commonly used by three- and two-toed sloths for food and resting are summarized for four habitat types in Table 5.

Statistical analysis

All statistical analyses were conducted using Statgraphics Plus 5.1 (Statistical Graphics Corp 1994–2001). The level of significance used to reject the null hypothesis was set at $P = 0.05$; for a few tests, a level of significance of $P = 0.10$ might be more appropriate. We used the *median* as a basis for estimating home range size (Kernall method) rather than the mean to minimize the impact of unusual individual animals that traveled very long distances. Home range sizes and frequencies of estimated distances traveled each year were contrasted between sexes using Kruskal–Wallis tests (Sokal and Rohlf *1995*).

Results

Habitat diversity and composition

Shannon–Wiener estimates of tree species diversity ranged from 0.89 to 3.84 per habitat, with the cacao agroforest having the least diversity and the adjacent riparian forest and living fences the greatest diversity. The riparian forest inventory contained 55 tree species, the living fences had 39 tree species, while the cacao plots and the pastures each contained 21 species (Table 2). Species richness estimates based on rarefaction analyses were highest in living fences and riparian forest segments (Fig. 3), but these were also the habitat types with the greatest density and numbers of woody plants. Our sampling was not exhaustive but clearly indicates that riparian forests and fence rows that mix introduced and native species have a more diverse woody plant flora than pastures and cacao agroforests. Cacao trees accounted for almost 80% of the woody plants in the cacao agroforests, while more than 50% of the cacao shade was *Leucaena leucocephala*, a factor that reduced the diversity estimate for this habitat type.

Table 2 Estimates of tree density, tree species richness and tree species diversity for four habitat types near Pueblo Nuevo de Guácimo, Limón, Costa Rica in 2006

	Habitat Type			
	Riparian forest	Pasture with isolated trees	Living fences	Cacao
Number of plots	15	5	12	15
Total plot area (ha)	0.75	5	0.9	0.57
Number of species	55	21	39	21
Number of treesa[a]	293	41	484	98
Density (trees/ha)[a]	391	8.2	538	172
Species diversity (H’)	3.84	2.74	2.88	0.89

[a]This cacao agroforest shade tree density estimate excludes *T. cacao*; the cacao spacing was approximately 3 × 3 m but drainage canals reduced the overall cacao density to 833 trees/ha

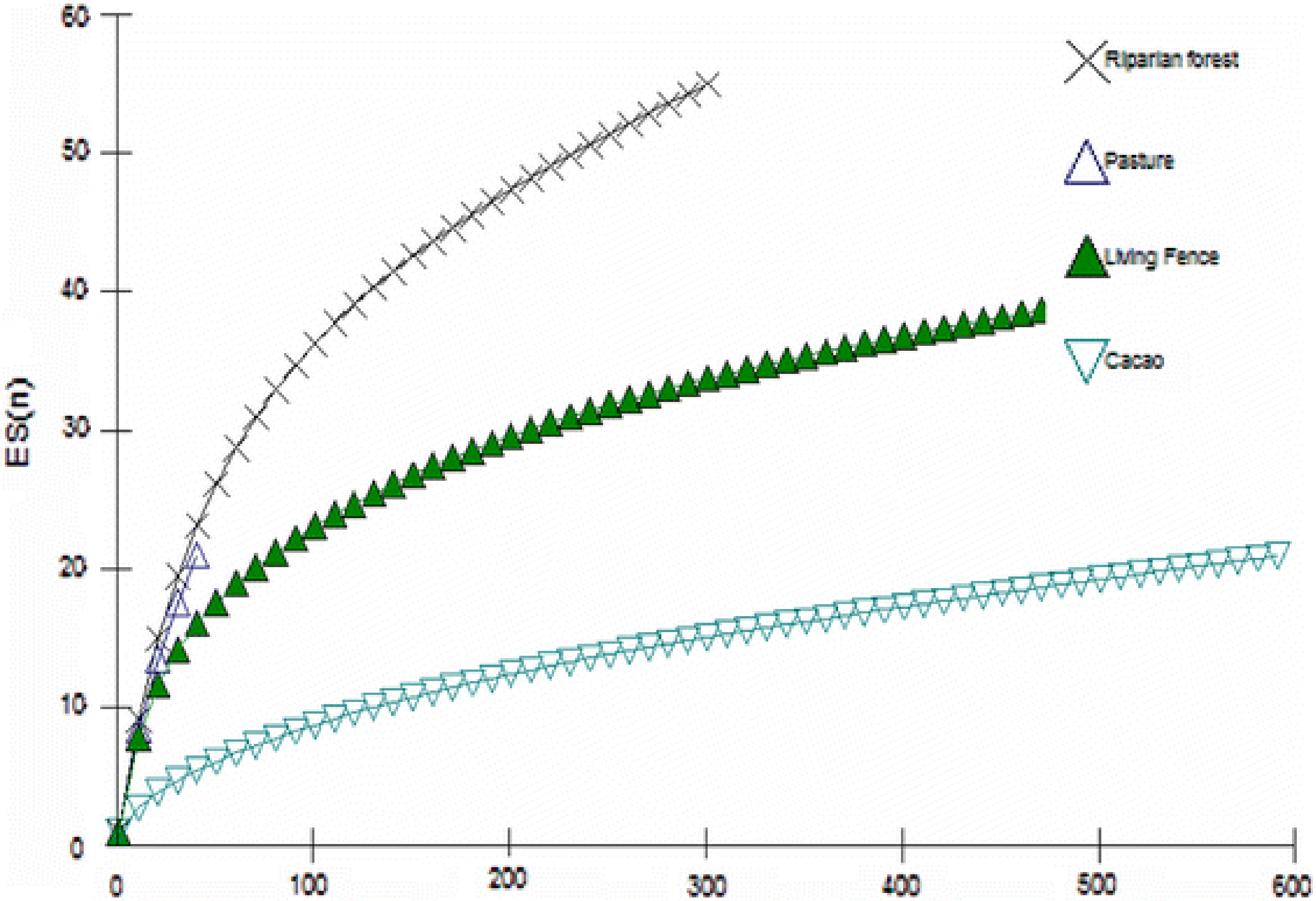

Fig. 3 Rarefaction curves estimated for woody plants in selected habitats near Nuevo de Guácimo, Limón, Costa Rica 2006

We identified a total of 85 tree species in four habitat types during the vegetation inventories. Additional species not included in the fixed area inventories were occasionally encountered during sloth relocations, especially in the riparian forests, but these were always less common species. Our inventories identified the most common species occurring in the major habitats (Table 3), but only a far more intensive sampling could identify all the species in species-rich habitats such as riparian forests. Not surprisingly, many of the most common trees in this landscape were introduced species (see Table 3); the most common tree (excluding *T. cacao*) was *Leucaena leucocephala*, which constituted 6.8% of the 1416 trees inventoried. Other common trees included *E. poeppigiana* (5.6%), *Ochroma pyramidale* (5.3%), *F. werckleana* (4.2%), *Eucalyptus globulus* (3.2%), *Gmelina arborea* (3.1%), *Cecropia obtusifolia* (2.9%), and *Cordia alliodora* (2.6%).

Table 3 Numbers of individuals of each of the 30 most common plant species present in riparian forests, pastures, living fences, and cacao agroforest in the agricultural landscape of Pueblo Nuevo de Guácimo, Limón, Costa Rica

	Habitat Type			
	Cacao	**Living fences**	**Pasture w/ isolated trees**	**Riparian forest**
Alchornea costaricensis	0	0	1	11
Carica papaya[b]	7	0	0	0
Castilla elastica[b]	0	4	0	15
Cecropia obtusifolia	0	33	0	8
Cederla odorata[b]	1	2	4	1
Cestrum racemosa	0	11	0	1
Cocos nucifera [a]	0	13	0	0
Cordia alliodora[b]	1	11	0	25
Erythrina poeppigiana[b]	0	37	9	33
Eucalyptus globulus [a]	2	43	0	0
Ficus werckleana	0	54	0	6
Genipa americana	0	1	1	12
Gliricidia sepium[b]	0	31	0	0
Gmelina arborea [a]	0	42	1	1
Hieronyma alchorneoides	0	0	1	0
Hura crepitans	0	1	0	9
Inga marginata	0	0	0	16
Inga oerstediana	0	6	4	19
Leucaena leucocephala[b]	54	42	0	0
Lonchocarpus fraxinus	0	0	2	9
Musa textilis [a]	6	0	0	1
Ochroma pyramidae	0	71	0	4

Pentaclethra macroloba	0	0	0	6
Piper auratum	5	0	0	0
Platymiscium pinnatum	0	22	0	0
Posoqueria grandiflora	0	1	0	11
Pterocarpus officinalis	0	0	1	1
Solanum umbellatum	0	1	0	1
Spondias mombin[b]	0	9	2	14
Theobroma cacao [a]	475	0	2	1
Trophis racemosa	0	5	3	11
Other species	49	37	10	91
Total number of trees	*600*	*477*	*41*	*307*

[a] Exotic

[b] Commonly planted native species

Sloth home range size

During 2004 and 2005, a total of 1296 location points were recorded for the 15 three-toed sloths, while a total of 1902 relocation points were recorded for the 12 two-toed sloths (Table 1). Home range estimates calculated using the 'fixed kernel home-range' procedure showed that male *B. variegatus* had a mean home range of 9.18 hectares (±53.07 s.d.) and females of 6.45 hectares (±9.26 s.d.). The difference was not significant (Kruskal–Wallis, *d.f = 1, 13;* H = 1.08, *P* = 0.29). By contrast, the median home range size for three-toed sloths was 5.2 hectares. Using the median as the home range estimate minimizes the effect of one unusual animal that traveled long distances, perhaps trying to establish a home range.

Male two-toed sloths had a mean home range of 21.52 (±56.59 s.d.) hectares and females of 1.69 (±24.71 s.d.) hectares, but this several-fold difference was not significant due to the very large standard errors associated with the estimates (Kruskal-Wallis, *d.f = 1, 10;* H = 2.38, *P* = 0.12). The median home range size for two-toed sloths was 4.4 hectares, smaller than the mean estimate for males but slightly larger than the mean estimate for females. We believe that use of the median as an estimate of home range size may provide a more accurate picture of typical sloth behavior, since occasional animals will move long distances.

Habitat use

During the study period, both sloth species moved between living fences, small patches of corn and secondary forest fragments, pastures, riparian forests and the cacao agroforest. Four habitats – cacao agroforests, living fence rows, pastures with isolated trees and riparian forests – accounted for the largest portion of the study landscape and recorded the majority of the sloth relocations. Both species of sloths appeared to establish home ranges that included portions of more than one habitat (Figs 1 and 2) and a few animals included parts of three or four habitats, thereby expanding the range of tree species available for feeding and resting. Two-toed and three-toed sloths established home ranges that occupied different portions of the study landscape, so 'potential available habitat' for each sloth species also varied. For example, cacao agroforests comprised only about 20% of the potential available habitat for three-toed sloths but represented almost 40% of the potential available habitat for two-toed sloths (Table 4).

Table 4 Potential available habitat (%) and observed and expected habitat use by three-toed (*Choloepus hoffmanni*) and two-toed *(Bradypus variegatus)* sloths in the agricultural landscape near Pueblo Nuevo de Guácimo, Limón, Costa Rica[a]. (Explain in the heading what the numbers in the observed use and the expected use columns refer to- the number of observed sightings in that habitat?)

Habitat type	Potential available habitat (%)	Three-toed Sloths[b]		Potential available habitat (%)	Two-toed Sloths[c]	
		Observed Use	Expected Use		Observed Use	Expected Use
Banana	1.4	3	18	3.0	16	58
Cacao	20.6	263	267	39.6	487	752
Corn field	0.9	7	11	1.9	8	37
Forest fragment	5.7	60	73	1.6	7	30
Living fence	3.3	119	43	4.6	406	87
Pasture	32.5	219	421	39.9	571	757
Pineapple	0.7	0	9	1.0	0	19
Riparian forest	35.0	625	454	6.3	306	120
Secondary forest	NA	NA	NA	2.0	97	38

Totals		1296	1296		1898	1898

[a]‘Expected use’ is the number of total recaptures that would occur in each habitat if sloths used habitats in the proportions available on the landscape. ‘Observed use’ is the actual number of recaptures that occurred in each habitat based on GPS relocations. Observed use of different habitats was significantly different from expected use for both two-toed and three-toed sloths as determined by Chi-square tests

[b]Chi-square statistic for observed versus expected habitat use by three-toed sloths; $\chi2 = 320.9$, d. f. = 7; $P < 0.0001$

[c]Chi-square statistic for observed versus expected habitat use by two-toed sloths; $\chi2 = 1778.4$; d. f. = 8; $P < 0.0001$

Within the potential available habitat for three-toed sloths, more than 88% occurred as riparian forests (35%), pastures (32.5%) and cacao (20.6%), with only 12% in other land uses (Table 4). Three-toed sloths appeared to form home ranges between 4 and 7 ha in size that contained fewer tree species than characteristic of two-toed sloths. Frequency distributions of three-toed sloth habitat use relative to the occurrence of habitats on the landscape indicate that cacao was used more or less in proportion to its availability, although three-toed sloths were never observed to feed on *Theobroma cacao*. Pasture and banana plantations were used substantially less then expected, while riparian forest and living fence rows were used more than expected (Table 4). Three-toed sloths were never observed entering pineapple plantations.

Almost 80% of the potential available habitat for two-toed sloths occurred as pasture (39.9%) and cacao agroforests (39.6 %), with all other land uses accounting for the other 20% (Table 4). As with the three-toed sloths, living fences and riparian forests were used more frequently than expected based simply on their availability, while cacao agroforests and pastures were used significantly less then expected. It is important to note that many sloths established home ranges that centered in the cacao agroforest but feeding usually occurred in adjacent fencerows and riparian forests. Two-toed sloths (or at least the females) established smaller home ranges of only about 2 ha based on median home range sizes but even small home ranges usually included parts of several habitat types. Relatively few relocations were made in bananas and forest fragments, but use of these habitats appeared to be less than expected based on occurrence, while pineapple appeared never to be used (Table 4).

Preferential tree resource use

Three-toed sloths visited a total of 71 tree species in all habitats, with 15 used as food, primarily fresh leaves and inflorescences. Not all tree species occurred in all habitats, but three-toed sloths appeared to return to specific trees that were preferred for feeding. The trees in which three-toed sloths were most frequently relocated included *Cecropia obtusifolia*, *Cecropia insignis*, *Coussapoa villosa*, *Ficus werckleana*, *Inga oerstediana*, *Luehea seemannii*, and *Nectandra salicifolia* (Table 5). Several species, such as *Ocotea sinuata* in pastures, and *Cecropia obtusifolia* in the cacao plots, were used much more frequently than their occurrence in those particular habitats would suggest, while other common trees within the potential available habitat, e.g. *Erythrina poeppigiana*, were seldom or never visited (Table 5). For example, although *Leucaena leucocephala* was the most common shade tree in the cacao agroforest (55.1% of all shade trees; Table 5), three-toed sloths were rarely observed in these trees and were never observed eating them. Three-toed sloths appeared to eat many fewer tree species than did two-toed sloths.

Table 5 Two- and three-toed sloth use (SU) of selected tree species by habitat based on GPS relocations, versus the availability (AV) of trees in each habitat type from inventory data. Numbers represent the total numbers of observations of sloths in each tree species within each habitat. Trees were used primarily for feeding (F) or resting (R). Some tree species were not found in sample plots in some habitats (NI); however, sloths were occasionally found using these species

	Tree Use	**Cacao**		**Living fence**		**Pasture with isolated tree**		**Riparian forest**	
		SU	**AV**	**SU**	**AV**	**SU**	**AV**	**SU**	**AV**
Three-toed sloths[c]									
Cecropia insignis	F, R	0	NI	42	NI	16	NI	27	NI
Cecropia obtusifolia	F, R	169	NI	16	33	5	NI	114	8
Coussapoa villosa	F, R	0	1	5	1	86	1	51	NI
Erythrina poeppigiana[b]	R	0	NI	8	37	5	9	3	33
Ficus werckleana	F, R	16	NI	15	54	5	NI	5	6
Goethalsia meiantha	F, R	1	NI	4	3	8	NI	4	3
Inga oerstediana	F, R	1	NI	1	6	5	4	21	19
Leucaena leucocephala[b]	R	0	54	0	42	0	NI	0	NI

Luehea seemannii	F, R	0	NI	1	1	6	NI	18	4
Nectandra salicifolia	F, R	1	NI	1	NI	0	NI	36	5
Ochroma pyramidale	R	12	NI	3	71	0	NI	7	4
Ocotea sinuata[b]	F, R	8	1	47	5	46	NI	34	5
Pterocarpus officinalis	F, R	0	NI	0	NI	11	1	65	1
Rollinia pittieri	F, R	1	NI	0	NI	2	NI	25	7
Samanea saman	R	19	NI	0	NI	0	NI	13	1
Theobroma cacao [a]	F, R	0	475	0	0	0	2	0	1
Total # of observations		*263*		*219*		*219*		*625*	
Total # of trees			*595*		*487*		*41*		*293*
Two-toed sloths[d]									
Cecropia obtusifolia	F, R	1	NI	10	33	5	NI	1	8
Cestrum racemosa	R	4	NI	15	11	28	NI	0	1
Cordia alliodora[b]	R	2	1	30	11	53	NI	14	25
Erythrina poeppigiana[b]	F, R	69	NI	159	37	102	9	14	33
Eucalyptus globules [a]	R	9	2	3	43	0	NI	0	NI
Ficus werckleana	R	1	NI	4	54	17	NI	13	6
Hura crepitans	F, R	0	NI	2	1	45	NI	107	9
Inga oerstediana	F, R	2	NI	5	6	37	4	24	19
Leucaena leucocephala[a]	R	51	54	0	42	0	NI	0	NI
Luehea seemannii	F, R	5	NI	1	1	9	NI	7	4
Ocotea sinuate	F, R	1	1	6	5	8	NI	3	5
Pentaclethra macroloba	R	0	NI	0	NI	10	NI	0	6

Pterocarpus officinalis	F, R	0	NI	9	NI	18	1	20	1
Solanum umbellatum	F, R	0	NI	6	1	6	NI	0	1
Spondias mombin[b]	F, R	6	NI	15	9	26	2	14	14
Theobroma cacao [a]	F, R	262	475	6	0	2	2	0	1
Trophis racemosa	F, R	6	NI	22	5	5	3	6	11
Total # of observations		487		406		571		306	
Total # of trees			595		487		41		293

[a] Exotic

[b] Commonly planted native species

[c]Differences in the 'use' of trees relative to their availability in a habitat was significant for three-toed sloths as determined by a Chi-square statistic; $\chi 2 = 19449.4$; d.f = 1; $P < 0.01$

[d]Differences in the 'use' of trees relative to their availability in a habitat was significant for two-toed sloths as determined by a Chi-square statistic; $\chi 2 = 5323.6$; d.f = 1; $P < 0.01$

Two-toed sloths visited 101 tree species and fed on 34 of them. The most frequently consumed tree parts/species included fresh leaves and inflorescences of *E. poeppigiana, Theobroma cacao, Hura crepitans, Leucaena leucocephala, Piper auratum, Hieronyma alchorneoides, Spondias mombin, Inga oerstediana*, and *Trophis racemosa*. Two-toed sloths also appeared to favor some species over others relative to their availability in several habitats. For example, two-toed sloths made intensive use of *E. poeppigiana* in cacao agroforests although the availability of this tree was low (<1%); *Cestrum racemosa, Cordia alliodora* and *Hura crepitans* were also frequented in the pastures although their availability also was relatively low, occasionally only a single individual (Table 5). Two-toed and three-toed sloths shared a food preference for a few species, including *Cecropia obtusifolia, Coussapoa villosa* and *Inga oerstediana* while many other species appeared to be used by one or the other but not both species, e.g., *Theobroma cacao* leaves were eaten by two-toed sloths (Table 5). Obviously, some individuals may feed on certain tree species while they were not observed, but a few species were clearly preferred, e.g. *Erythrina poeppigiana* and *Leucaena leucocephala* by two-toed sloths.

Discussion

Habitat use

Four habitat types (cacao agroforests, living fence rows, pastures with isolated trees, and riparian forests) account for approximately 90% of the ‘potential available habitat’ for two- and three-toed sloths in our study (Table 4). Riparian forest segments and living fence rows were used by two-toed and three-toed sloths at frequencies greater than expected, probably because they contained relatively high diversities and densities of preferred food species such as *Cecropia*, *Ficus*, *Inga* and *Ocotea* (Table 5). Two-toed sloths also used secondary forest more often than expected, but relatively few captures or subsequent relocations of collared sloths were made in this habitat type.

Cacao agroforest was used by three-toed sloths more or less in proportion to its occurrence on the landscape, while two-toed sloths used cacao agroforest somewhat less than expected given its availability (Table 4). At least some of this differential habitat use appears to relate to the relative abundance in different habitats of preferred species for feeding, but other factors such as predator avoidance are probably important as well. Despite their substantial use of cacao agroforests, three-toed sloths were never observed feeding on cacao leaves or pods. Their use of cacao agroforest appeared to center on the presence of a few preferred food trees such as *Cecropia*, *Coussapoa* and *Ocotea*, but three-toed sloths spent most time in riparian forest and fence row habitats adjacent to the cacao agroforest within their potential available habitat.

Two-toed sloths used cacao agroforests somewhat less than expected based on estimates of ‘potential available habitat’ (Table 4), but they were frequently observed feeding on cacao as well as several other species (Table 5). Farmers often identify primates as well as squirrels as predators on cacao but sloths are seldom noted. In this study, the cacao agroforest seemed to provide refuge for the two-toed sloths as three radio-collared males remained here for long periods without ever leaving. The cacao agroforest we studied has a cable system for moving harvested cacao pods to a central processing facility (similar to many banana plantations). Two-toed sloths were seen using the cable system on a nightly basis to move between feeding and resting sites in the cacao agroforest. One male two-toed sloth (#48) moved approximately 1,500 m in one night along the cables. However, three-toed sloths do not appear to use this cable network. In one respect, the less-than-expected use of the cacao agroforest by two-toed sloths is surprising given the high density of preferred *Erythrina* and *Leucaena* trees within this habitat.

Riparian forests had the greatest species diversity and richness (Table 2) and might be expected to attract more sloths based simply on the high frequencies of preferred food species (Table 3). Living fence rows had a moderately high diversity of woody plants but some of these species e.g., *Erythrina poeppigiana*, are preferred for feeding only by two-toed sloths. It is not obvious whether a high tree species diversity *per se* makes some habitats attractive to sloths or whether some combination of structural features, e.g., density of trees, connections to other landscape features, together with preferred food species, can account for this differential habitat use. Ramirez, Vaughan and Herrera (in review) found that mothers with young sloths make extensive use of riparian forests probably because preferred tree species are readily available in these habitats. However, protection from predators in this high density forest might also account for sloth use of riparian forests during this critical period in juvenile's lives.

Chacon and Harvey (*2006*) estimated that living fences constitute <2% of the landscape near Rio Frio, Costa Rica, but appeared to provide important connectivity features on a landscape dominated by pasture. Williams and Vaughan (*2001*) found capuchin monkeys (*Cebus capucinus*) made extensive use of a network of living fences for travel, resting and feeding on a cattle ranch in western Costa Rica. Living fence rows were only a small part of the total available habitat for sloths but this habitat was used far more often than would be expected given its sparse distribution (Table 4). Fence rows comprised only 4.6% of the potential habitat available to two-toed sloths but 21.3% of their relocations occurred in living fence rows. A similar pattern was found for three-toed sloths; living fence rows comprised only 3.3% of their potential habitat but 9.2% of the relocations occurred here (Table 4).

Living fences are obviously important for sloth movements into and out of cacao and riparian forests. Harvey et al. (*2004*, *2005b*) suggested that living fence rows should form part of any biodiversity strategy at a landscape level. Our results indicate that living fence rows are indeed important for sloth conservation, especially for two-toed sloths. One danger faced by sloths was pollarding of living fence rows, which occurred three times a year, especially near cattle pastures. This caused sloths to temporally leave the area and also restricted travel to certain routes. Since this study, pollarding has been suspended but not pollarding is probably impractical in the long term. Fence rows that grow into large trees are not likely to find favor in many agricultural settings. Methods of timing the pollarding, or limiting it to only some trees in each cycle, need to be developed to ensure that agricultural benefits as well as conservation benefits are achieved.

Pasture was the second most commonly used habitat by both sloths, but its use was still less than expected given its common occurrence in the landscape (Table 4). Individual sloths did visit particular trees of preferred species in pastures, especially *Erythrina poeppigiana*, often traveling considerable distances to reach these trees. Several sloths were observed to repeatedly visit the same tree over several months time, always for feeding even though the distances separating some preferred trees in this habitat were often hundreds of meters. Deforestation and pasture formation without trees likely place sloths at a disadvantage because they are exposed to potential predators when they move on the ground between trees.

Local farmers identify dogs, coyotes (*Canis latrans*), feral cats and humans as predators. Two radio-collared three-toed sloths and one two-toed sloth were preyed upon and killed near the cacao agroforest borders. However, two-toed sloths frequently rested on the ground, especially in dense grass in pastures where the humidity is high. We believe that the distances separating preferred trees and the risks posed by travel on the ground account for the lower than expected use of this habitat by sloths.

All other habitats, including banana and pineapple monocultures and secondary forest fragments appeared to be used by sloths less often than expected (Table 4). The finding that secondary forest fragments were not well used may simply be due to their relatively limited occurrence (only 0-2% of the landscape) and/or lack of preferred tree species, but no detailed inventories of trees were conducted here. Sloths were observed in a few of these fragments but they were not captured and radio collared so we have little information on the value of this particular habitat.

Preferred tree use

Inside the cacao agroforests, adjacent riparian forests and fence rows, the three-toed sloth found food sources such as *Cecropia obtusifolia, Coussapoa villosa, Nectandra salicifolia and O. sinuata* (Table 5); all of these species are present in cacao agroforests and other land uses in this region. It is important to note that these trees were often the only representatives of these species in the sampled habitat (Table 3), but some sloths returned to these trees repeatedly, especially for feeding. We believe that the agricultural landscape could be more valuable for conservation purposes if it included more of the species that appear to serve as important resting places or food sources for two- and three-toed sloths (Table 5). We have observed up to five three-toed sloths in the same *Cecropia* tree for more than a month until the tree was totally defoliated. On another occasion, up to five two-toed sloths were observed in the same *Hura crepitans* tree for several days, after which they all moved to another nearby *Hura crepitans*. Given the large amount of time spent feeding each day, it is difficult to overestimate the importance of preferred food species as central to sloth conservation. Some preferred tree species undoubtedly would have value for other animals as well.

Home-range size and patterns of home range use

Sunquist and Montgomery (1978) studied habitat selection and its use by *C. hoffmanni* and *B. variegatus* in a forested landscape in Panama and found home ranges usually comprised less than two hectares. Chiarello (*1998*) reported that *B. torquatus* individual home ranges varied from 0.6 to 6 hectares in the Brazilian Atlantic forest. Our estimates of the median home range size for two-toed (4.4 ha) and three-toed (5.2 ha) sloths are in reasonable agreement with these earlier estimates. Our estimates of home range size may be slightly larger than earlier estimates given that our telemetry data used in home range estimates spans more than one year for some animals. Montgomery and Sunquist (*1978*) indicated that both sloth species used several tree species for feeding and resting. Three-toed sloths are recognized as generalists but most individuals studied here appear to specialize more than two-toed sloths in their preferred food species. Freeland and Janzen (*1974*) noted that sloths avoided widely separated individual trees because moving between trees implied high energy costs. Our finding that individual sloths may repeatedly cross pasture to reach preferred food species casts doubt on this hypothesis.

We observed several sloths navigating relatively long distances to reach a favored resource, such as *Coussapoa villosa*, *Hieronyma alchorneoides* or *Pterocarpus officinalis*. Home ranges for two-toed sloths in this study were perhaps more a function of establishing defensible territories rather than accessing specific resources. Occasionally, we observed individuals of both sloths species sharing the same tree for resting or feeding. Beebe (*1926*) and Montgomery and Sunquist (*1978*) never observed more than one three-toed adult sloth in the same tree simultaneously. Aggressive behavior appears common between three-toed and two-toed sloths, perhaps during territorial disputes or resource defense (Green 1989), but our observations suggest that co-existence is possible at least during certain times of the year.

Implications for Sloth Conservation

We found that a mosaic of cacao agroforests and other land uses containing trees can support a sizeable population of two- and three- toed sloths. In two, 1 week periods in both 2005 and 2006, we captured 54 and 57 different sloths inside of (or within 100 m of) the cacao agroforest for health assessments (Vaughan et al. *2006*). We believe that there may be twice that many sloths currently using this mosaic of cacao agroforest, living fence rows and riparian forest strips as a refuge, for breeding and for feeding. It seems clear that providing a mosaic of habitats containing arboreal elements is important for sloth conservation on agricultural landscapes. Despite having home range sizes of only a few hectares, almost all sloths studied here included at least two or three different habitats containing trees within their home ranges. This may be true simply because no single habitat can provide the diversity of food species and resting sites required. However, the large numbers of sloths that occupy this landscape are able to adapt to this highly disturbed environment by exploiting the corridor-like arboreal elements along streams, living fencerows and within cacao agroforests. Sloths will travel considerable distances in open habitat such as pasture to reach preferred tree species, but this obviously entails a significant risk of predation.

Given current landscape use in Limón province, the diversity of habitat types available and the natural history of sloths, we believe that a relatively small number of easily achievable actions would enhance the prospects for conserving biodiversity well beyond the two species studied here. Three-toed sloths used the cacao agroforest and contiguous habitats, often appearing to establish a base in the cacao agroforest from which they ventured into the other habitats. Most home ranges that centered within the cacao agroforest also included living fence and/or riparian forest as part of a mosaic of habitats, even for home ranges less than 1 ha in size. Ensuring that the arboreal elements of this mosaic remain intact is our primary concern and the basis for most of our recommendations.

First, an adequate number of preferred tree species should remain available on agricultural landscapes as a source of food, resting sites and other important activities. The task of maintaining or expanding the numbers of preferred tree species may be as simple as directing farm workers to retain a few saplings of certain species during the periodic cleanings of cacao agroforests and fencerows. Tree species that would benefit two- and three-toed sloths in living fence rows include *Cecropia obtusifolia, Cordia alliodora, Erythrina poeppigiana (*whose leaves are commonly used for cattle forage*), Ficus werckleana*, *Ocotea sinuata and Spondias mombin*, but not *Gmelina arborea* and *Ochroma pyramidale*. In the cacao agroforest, favored species should include *Cecropia obtusifolia*, *Coussapoa villosa, Erythrina poeppigiana, Ficus werckleana* and several *Inga* species, but not *Eucalyptus globulus.* Some trees commonly used for cacao shade, including *Cordia alliodora* and *Leucaena leucocephala,* are visited by sloths but these do not appear to be favored as a food source. In our experience, species such as *Erythrina poeppigiana* probably do not need extra effort to maintain their presence, but species such as *Coussapoa villosa, Ficus werckleana, Hura crepitans* and *Ocotea sinuata* would likely benefit from a greater awareness of their value to wildlife. Riparian forests are the most diverse habitat type on this landscape and simply allowing them to regenerate and maintain relatively natural conditions would be sufficient to maintain this important habitat. *Trophis racemosa, Spondias mombin* and *Inga* species are among those tree species which provide food in the form of leaves for sloths and fruit for birds and other mammals and should be widely planted.

Second, we believe that even greater use would be made of preferred trees in large pastures if tree densities there were slightly greater, thereby affording more resting sites. Obviously, pastures are managed for forage, not trees, but isolated trees are used not only by sloths but by a host of other species, especially raptors, so they serve a valuable role in biodiversity conservation. If only a few individuals and species are to be retained in pastures, we suggest that preferred food species such as *Coussapoa villosa*, *Hieronyma alchorneoides, Hura crepitans* and *Pterocarpus officinalis* be favored; some of these species are also valuable hardwoods.

Third, we have observed that the periodic pollarding and cleaning of living fence rows temporarily displaces sloths. We suggest that different schedules for pollarding living fences be established so that some trees/rows are always available to sloths. Living fence rows appear to be heavily used by sloths for feeding and travel, so ensuring that these corridors are not broken or even temporarily unavailable is an important conservation concern.

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References

Beebe W (1926) The three-toed sloth *Bradypus cuculliger*. Wagner Zool (New York) 7:1–67

Chacon M, Harvey CA (2006) Live fences and landscape connectivity in a neotropical agricultural landscape. Agroforest Sys 68:15–26
SpringerLink

Chiarello AG (1998) Activity budgets and ranging patterns of the Atlantic forest maned sloth *Bradypus torquatus* (Xenarthra: Bradypodidae). J Zool 246:1–10
crossref

Chiarello AG, Chivers D, Bassi C, Maciel MAF, Moreira LS, Bazzalo M (2004) A translocation experiment for the conservation of maned sloths, *Bradypus torquatus* (Xenarthra, Bradypodidae). Biol Conserv 118:421–430
crossref

Eisenberg JF, Thorington RW (1974) A preliminary analysis of a neotropical mammal fauna. Biotropica 5(3):150–161
crossref

FAO (2004) FAOSTAT-Agriculture. Food and Agriculture Organization of the United Nations. http://faostat.fao.org/faostat. Cited 3 August 2005

Freeland WJ, Janzen DH (1974) Strategies in herbivory by mammals: the role of plant secondary compounds. Am Nat 108:269–289
crossref ChemPort

Genoways HH, Timm RM (2003) The Xenarthrans of Nicaragua. J Neotrop Mammal 10(2):231–253

Greenberg R, Bicher P, Cruz Angon A (2000) The conservation value for birds of cacao plantations with diverse planted shade in Tabasco, Mexico. Anim Conserv 3:105–112

Guiracocha G (2000) Conservacion de la biodiversidad en los sistemas agroforestales cacaoteros y bananeros de Talamanca, Costa Rica. MSc. Thesis, Centro Agronomico Tropical de Investigacion y Ensenanza, Turrialba, Costa Rica

Guiracocha G, Harvey CA, Somarraba E, Krauss E, Carrillo E (2001) Conservación de la biodiversidad en sistemas agroforestales con cacao y banano en Talamanca, Costa Rica. Agroforestería en las Amér 8(30):7–11

Harvey C, Tucker N, Estrada A (2004) Live fences, isolated trees, and windbreaks: Tools for conserving biodiversity in fragmented landscapes. In: Schroth G, da Fonseca G, Harvey C, Vasconcelos H, Gascon C, Izac A (eds) Agroforestry and Biodiversity Conservation in Tropical Landscapes. Island Press, Washington, D.C. pp 261–289

Harvey CA, Alpizar F, Chacon M and Madrigal R (2005a) Assessing linkages between agriculture and biodiversity in Central America: Historical overview and future perspectives. Mesoamerican & Caribbean Region, Conservation Science Program. The Nature Conservancy (TNC). San José, Costa Rica, 140 p

Harvey CA, Villanueva C, Villacís J et al (2005b) Contribution of live fences to the ecological integrity of agricultural landscapes in Central America. Agriculture Ecosystems and Environment 111:200–230

Harvey CA, Gonzalez J, Sommariba E (2006) Dung beetle and terrestrial mammal diversity in forests, indigenous agroforestry systems and plantain monocultures in Talamanca, Costa Rica. Biodiv Conserv 15:555–585

Hellmann JJ, Fowler GW (1999) Bias, precision, and accuracy of four measures of species richness. Ecol Appl 9:824–834

Helmuth JG, Lambin F (2002) Proximate causes and underlying driving forces of tropical deforestation. BioScience 52(2):143–150
<Occurrence Type="DOI"><Handle>10.1641/0006-3568(2002)052[0143:PCAUDF]2.0.CO;2</Handle></Occurrence>

Holdridge LR (1964) Life zone ecology. Tropical science center, San Jose, Costa Rica, 206p

James FC, Rathbun S (1981) Rarefaction, relative abundance, and diversity of avian communities. Auk 98:785–800

Kessler M, Kebler PJ, Gradstein SR, Bach K, Schmull M, Pitopang R (2005) Tree diversity in primary forest and different land use systems in Central Sulawesi, Indonesia. Biodiv Conserv 14(3):547–560

Leston D (1970) Entomology of the cocoa farm. Ann Rev Entomol 15:273–294

McNeely J, Schroth G (2006) Agroforestry and biodiversity conservation – traditional practices, present dynamics, and lessons for the future. Biodiv Conserv 15(2):549–554

Montgomery GG, Sunquist ME (1975) Impact of sloths on neotropical forest energy flow and nutrient cycling. In: Golley FB, Medina E (eds) Tropical ecological systems: trends in terrestrial and aquatic research ecological studies, (Vol 11). Springer-Verlag, New York, pp 69–98

Montgomery GG and Sunquist ME (1978) Habitat selection and use by two-toed and three-toed sloth. In: Montgomery GG (eds). The Ecology of Arboreal Folivores Smithsonian Inst. Press, Washington, D. C., pp 329–359

Neu CW, Byers CR, Peek JM (1974) A technique for analysis of utilization-availability data. Journal of Wildlife Management 38:541–545

Reitsma R, Parrish J, McLarney W (2001) The role of cacao plantations in maintaining forest avian diversity in southeastern Costa Rica. Agroforestr Syst 53:185–193

Rice RA, Greenberg R (2000) Cacao cultivation and the conservation of biological diversity. Ambio 29 (3):167–173
<Occurrence Type="DOI"><Handle>10.1639/0044-7447(2000)029[0167:CCATCO]2.0.CO;2</Handle></Occurrence>

Roth D, Perfecto I (1994) The effects of management systems on ground-foraging ant diversity in Costa Rica. Ecol Appl 4(3):423–436

Ramirez O, Vaughan C, Herrera G (in review) Temporal and spatial ecology of female Three-toed Sloths (*Bradypus variegatus)* and their young in an active Costa Rican cacao (*Theobroma cacao)* plantation

Ruf F, Schroth G (2004) Chocolate forests and monocultures: a historical review of cocoa growing and its conflicting role in tropical deforestation, forest conservation. In Schroth G, da Fonseca G, Harvey C, Vasconcelos H, Gascon C and Izac A (eds) Agroforestry and biodiversity conservation in tropical landscapes. Island Press, Washington, D.C., pp 107–134

Sánchez-Azofeifa GA, Harris R, Skole D (2001) Deforestation in Costa Rica: A quantitative analysis using remote sensing imagery. Biotropica 33(3):378–384

Seaman DE, Millspaugh JJ, Kernohan BJ, Brundige GC, Raedeke KJ, Gitzen RA (1999) Effects of sample size on kernel home range estimates. J Wildl Manage 63:739–747

Schroth G, da Fonseca G, Harvey CA, Gascon C, Vasconcelos HL, Izac A (2004) Introduction: the role of agroforestry in biodiversity conservation in tropical landscapes. In: Schroth G, da Fonseca G, Harvey C, Vasconcelos H, Gascon C, Izac A (eds) Agroforestry and biodiversity conservation in tropical landscapes. Island Press, Washington, D.C., pp 1–14

Sokal RR, Rohlf FJ (1995) Biometry, 3rd edn. W. H. Freeman and Co., New York, 885p

Sunquist ME, Montgomery GG (1973) Activity patterns and rates of movement of two-toed and three-toed sloths (*Choloepus hoffmanni* and *Bradypus infuscatus*). J Mammal 54:946–954

Swihart RK, Slade NA (1997) On testing for independence of animal movements. Journal of Agricultural Biological and Environmental Statistics 2:48–63

Tilman D, Cassman K, Matsons P, Naylor R, Polasky S (2002) Agricultural sustainability and intensive production practices. Nature 418:671–677

Vaughan C, Siudak-Campfield, J, Handley C, Paul-Murphy J, Ramirez O, de la Cruz E, Gross J, Herrera G, Jimenez M, Weaver S, Sladky K (2006) Preliminary assessment of ecosystem health in a highly modified neotropical agroecosystem using select wildlife species as indicators. First International Ecohealth Symposium, Madison, WI

Waltert M, Mardiastuti A, Mühlenberg M (2004) Effects of land use on bird species richness in Sulawesi, Indonesia. Conserv Biol 18:1339–1346

Wetzel RM (1985) The identification and distribution of recent Xenarthra (Edentata). In: Montgomery GG (ed) The evolution and ecology of armadillos, sloths, and vermilinguas. Smithsonian Institution Press, Washington, DC, pp 5–21

Wetzel RM, de Avila-Pires FD (1980) Identification and distribution of the recent sloths of Brazil (Edentata). Rev Braz Biol 40:831–836

White GC, Garrott RA (1990) Analysis of radio-tracking data. Academic Press, Inc., San Diego, California, 383 p

Williams H, Vaughan C (2001) White-faced monkey (*Cebus capucinus)* ecology and management in neotropical agricultural landscapes during the dry season. Rev Biol Trop 49(3–4):1192–1206