Tropical Zoology, 2023
Vol. 36 | Issue 1-2 | 1-20 | doi:10.4081/tz.2023.118

Post-release ecology of rehabilitated Hoffmann’s two-toed sloths in Panamá

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Received: 26 June 2022; Accepted: 8 June 2023.

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Abstract: The field of wildlife rescue and rehabilitation continues to grow as human expansion increases the rate of deforestation in Latin America. Sloths (*Bradypus* spp. and *Choloepus* spp.) are often admitted to rescue centers throughout Latin America due to their poor dispersal abilities and vulnerability to anthropogenic impacts. Although post-release monitoring is fundamental to measuring the success of wildlife rescue programs, few studies have assessed the outcomes of releasing hand-reared sloths back into the wild. We studied the ecology of rehabilitated and relocated Hoffmann’s two-toed sloths (*Choloepus hoffmanni*) in central Panamá during 2019-2020. Eleven two-toed sloths rescued from the wild were hand-reared in captivity for 727±193 days and then radiomarked, placed in an outdoor 500 m^2 soft-release enclosure for 3 months, and released in a nearby national park. While in the soft-release enclosure, two-toed sloths spent 80.0% of their time resting and became active and more alert in the evening (p=0.01). Upon release into the wild, two-toed sloths traveled a mean linear distance of 82.3±21.6 m and a mean distance of 25.6±9.5 m between successive radiolocations. The mean home range size was 2.92±1.19 ha, with females occupying larger areas than males. Two-toed sloths used trees with a smaller dbh than available (p≤0.001; p≤0.015) and selected trees with dense crowns and ≥50% lianas. Eight mortalities were recorded, with predation and natural causes being the main causes of mortality. Monthly survival was 0.72±0.14 and did not differ (p≤0.30) between males (1.00±0.00) and females (0.44±0.22). Rehabilitated two-toed sloths exhibited behavioral and space use patterns similar to wild two-toed sloths, with the exception of having lower survival rates following release in the wild. Our study provides information that can be useful in evaluating the efficacy of sloth rescue and rehabilitation programs throughout Latin America.

Key words: two-toed sloth; rescue; rehabilitation; Neotropical, Panamá.

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Introduction

Wild animals are often rescued from displacement, becoming orphaned, or sustaining injuries from domestic animal attacks or human-related activities (Shine and Koenig 2001; Saran et al. 2011; Pyke and Szabo 2018). These animals are then rehabilitated in captivity until considered suitable for release back into the wild (Miller 2012; IUCN/SSC 2013). The purpose and benefits of wildlife rehabilitation are heavily criticized in the conservation field, given the few studies of post-rehabilitation ecology and the resources used to focus on the welfare and recovery of individual animals (Kelly et al. 2010; Saran et al. 2011; Pyke and Szabo 2018). However, as human activities threaten the future of many species, wildlife rescue and rehabilitation continues to grow in popularity and is practiced worldwide (Martínez et al. 2004; Wimberger et al. 2010; Romero et al. 2019).

In some cases, wild animals that do not require treatment or rehabilitation in captivity are simply translocated from one area and released into another (IUCN 2013). Translocation efforts are conducted under various circumstances that may range from the reintroduction of an endangered species (Servanty et al. 2014) to the movement of animals to minimize human-wildlife conflicts (Imam et al. 2002; Goodrich and Miquelle 2005; Weise et al. 2015). Many failed attempts at translocation in the past have deemed it an unfavorable conservation practice (Fischer and Lindenmayer 2000; Athreya et al. 2011). Some unsuccessful cases have resulted in translocated animals dispersing back to capture sites and high mortality rates for reintroduced individuals (Athreya et al. 2011; Moseby et al. 2011). Despite these concerns, translocation efforts have proven effective in reducing human-wildlife conflicts and recovering species that are impacted by large-scale human-development operations (Vié 1999; Imam et al. 2002; Goodrich and Miquelle 2005; Weise et al. 2015; Swan et al. 2019). There are many cases, however, where animals are not able to be immediately reintroduced back into the wild due to medical or behavioral concerns which may impact survival (Martínez et al. 2004; Swan et al. 2019).

Sloths (*Bradypus* spp. and *Choloepus* spp.; order Pilosa) are often subjects of rescue and rehabilitation in Latin America (Chiarello et al. 2004; Larrazábal 2004; Martínez et al. 2004). Sloths are arboreal mammals that rely strictly on the canopy of tropical forests for food and habitat (Montgomery and Sunquist 1978). Described as specialists among arboreal folivores, sloths play an important role in nutrient cycling and support a series of mutualisms throughout neotropical ecosystems (Mendoza et al. 2015). Not only do sloths contribute to energy flow in the forest by providing nutrients and minerals to trees via fecal deposition, they also harbor a complex ecosystem within their fur, comprised of pyralid moths (*Cryptoses* spp.), microorganisms, and green algae (*Trichophilus* spp.) (Montgomery and Sunquist 1975; Pauli et al. 2014). One of the more disadvantageous characteristics of sloths is their incredibly low rate of movement due to their low metabolism and energy-poor diet, making them especially sensitive to deforestation and human development (Montgomery and Sunquist 1978; Chiarello 2008). In Latin America, sloths are frequently admitted to rescue centers for medical treatment from trauma, relocation from urban areas, and as orphans requiring long-term care in captivity (Chiarello et al. 2004; Larrazábal 2004; Martínez et al. 2004; Plese et al. 2016). Being a species with poor dispersal ability, studies support the presumption that loss of habitat will increase the need for sloth rescue and rehabilitation (Martínez et al. 2004; Peery and Pauli 2014; Dünner and Pastor 2017; Garcés-Restrepo et al. 2018).

Further assessment is needed on the post-release behavioral adaptations, habitat use, movement patterns, and survival of rehabilitated two-toed sloths *Choloepus hoffmanni* to aid rescue and rehabilitation programs (Plese and Chiarello 2014). Yet, given the strong

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interest in rehabilitating sloths throughout Latin America, to our knowledge, there are no published studies that have assessed post-release ecology of hand-reared, rehabilitated two-toed sloths (Dünner and Pastor 2017). We studied the ecology of Hoffmann's two-toed sloths rescued from the wild, hand-reared in captivity, and released into the wild. Our objectives were to: i) quantify activity budgets of individuals prior to release in the wild, ii) analyze movement patterns and estimate home range sizes, iii) assess habitat selection, and iv) determine survival rates and causes of mortality. Our goal was to provide information to assess the efficacy of sloth rescue and rehabilitation programs throughout Latin America.

Study area

The Pan-American Conservation Association (APPC) Rescue Center is located in Gamboa, Colón Province, Panamá, 1.2 km from the Gamboa Rainforest Reserve adjacent to Gatun Lake (Canuto 2008; Figure 1). The study area lies in the buffer zone of Soberanía National Park in the Panama Canal Watershed at 9°N latitude. Soberania National Park contains 22,104 ha of protected land consisting of mature tropical moist forest (Condit et al. 2001; Canuto 2008). This region has a dry season during late December to early April and a wet season during late April to mid-December with a mean precipitation of 234.5 mm and a mean temperature of 25.7°C (Condit et al. 2001; Canuto 2008; Harris et al. 2020). Forests are composed of humid semideciduous lowland forest with a dense understory of bromeliads, tree saplings, and lianas (Condit et al. 2001). In well-drained sites, the closed canopy reaches 20 to 40 m tall with emergent trees reaching >50 m, most of which are considered pristine, old-growth trees that have thrived from a lack of human disturbance (Condit et al. 2001). In the entire canal corridor >950 species of trees and shrubs have been identified, and 470 species can be found in the central isthmus of Soberanía. The forests surrounding the soft-release enclosure are suitable habitat for two-toed sloths as they contain a high diversity of tree species and lianas, two critical habitat characteristics which provide ample food availability and support horizontal and vertical displacement (Montgomery and Sunquist 1978).

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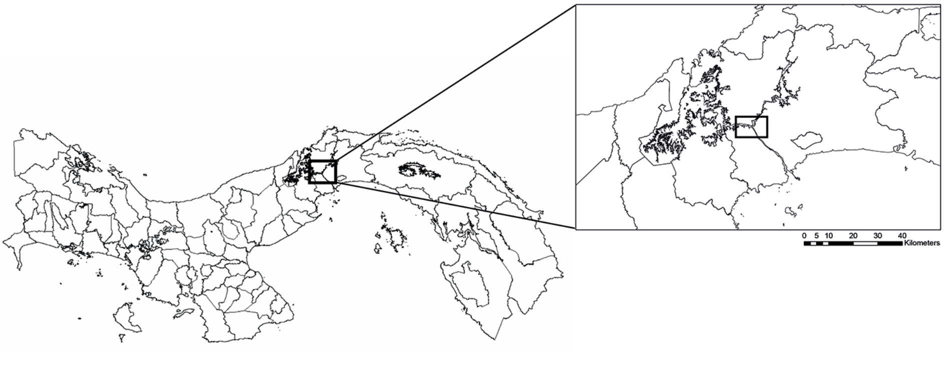

Figure 1. Study area where rehabilitated Hoffmann's two-toed sloths were released and radiotracked, Gamboa, Colón Province, Panamá, October 2019-October 2020.

Materials and Methods

General procedure

Eleven two-toed sloths born and rescued from the wild were rehabilitated in captivity at APPC facilities and processed into two groups. The first group consisted of three individuals that were radiomarked and placed in a soft-release enclosure during 31 October 2019-3 February 2020. Behavioral observations were conducted while sloths were inside the soft-release enclosure during that time. The first group of sloths was then released in adjacent Soberanía National Park and radio-tracked for movement trajectories, habitat selection, and survival. A second group of eight individuals was radiomarked and placed in the soft-release enclosure during 22 March 2020-22 June 2020. Behavioral observations were also conducted on these sloths and then released in Soberanía National Park and monitored as for the first group.

Husbandry and radio-marking of captive sloths

Prior to moving to the soft-release enclosure, two-toed sloths rescued from the wild were housed separately in 5 m x 3 m x 3 m pens at the APPC Sloth Sanctuary facility in Gamboa, Panamá for 727±193 days (mean ± SE value across all sloths). These animals were 1-6 years old and a mixture of males and females. Within each captive pen, tree branches, trunks and vines were assembled to provide ample space for sloths to move and forage. Eight-quart rubber bins filled with water were available, and sloths were fed twice daily with vegetables and leaves. Feedings during 1000-1300 hr included 4.0 g of boiled carrots, chayote, and green beans per sloth. Natural browse (700-1,000 g/sloth) was cut from the surrounding area and fed to sloths between 1700-1800 hr. Tree species used as natural browse were mango (*Mangifera indica*), ciruelo/jocote (*Spondias purpurea*), West Indian Elm (*Guazuma ulmifolia*), guácimo colorado (*Luehea seemannii),* gumbo limbo (*Bursera simaruba*), buttercup tree (*Cochlospermum vitifolium*), jobo (*Sponidas mombin L.*), and espavé (*Anacardium excelsum*). These tree species were selected due to their availability and abundance throughout the forested areas where sloths would be released. The plants were then hung in random locations within the enclosure to encourage two-toed sloths to forage independently. When natural browse was scarce, spinach, mustard greens, and bok choy was used as supplemental feeding.

When necessary, two-toed sloths were handled by two trained APPC keepers by grabbing the front and back limbs and allowing the sloth to hold onto the handler. Immediately prior to soft release, each sloth was measured, weighed, and sexed by examining the external genitalia (McCrane 1966, Meritt 1985). Two-toed sloths were then aged as juveniles or adults based on age and body weight (Meritt 1985). Two-toed sloths were fitted with a VHF radio-transmitter harness (Model TXF-325B, Telenax, Playa del Carmen, Mexico) weighing approximately 50 g. Each two-toed sloth was given a different color tape on its harness to identify individuals visually without the use of radiotelemetry. Two-toed sloth husbandry, handling, and tracking were conducted as approved by Institutional Animal Care and Use Committee protocol #19-017 at Southern Illinois University Carbondale.

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Soft release and activity budgets

During the soft-release period, we expected two-toed sloths to develop behaviors to improve their survivorship skills, such as acquiring food, finding shelter, and navigating an unfamiliar environment (Kleiman 1989). The goal of quantifying activity budgets of sloths during soft-release was to determine if, while being dishabituated from humans, rehabilitated sloths would exhibit similar, natural behaviors as described in wild sloths. Following radio-marking, two-toed sloths were placed ≥20 m apart on different habitat structures in the soft-release enclosure. The soft-release enclosure was a 500 m^2 outdoor area enclosed by a 1.40 m concrete wall with a predator fence surrounding the perimeter (Figure 2). The predator fence had 4 rows of aluminum wire mounted onto 1.45 m tall plastic ground stakes, with one steel door to allow APPC staff-authorized access. Vegetation within the soft release enclosure included gumbo limbo, buttercup tree, jobo, trumpet tree (*Cecropia obtusifolia*), and barrigón (*Pseudobombax septenatum)*, with an understory vegetation of lantana (*Lantana* spp.*)* and purple morning glory (*Ipomoea purpurea*). Natural browse (700-1,000 g/animal) was placed within the enclosure 5 times a week as a supplement, and included mango, guácimo colorado, buttercup tree, gumbo limbo, ciruelo and espavé. Several 8-quart rubber bins filled with water were also available.

Behavioral observations of two-toed sloths within the soft-release enclosure were conducted 5 days a week. Focal sampling with continuous recording was used to quantify activity budgets, measuring true frequencies and durations of behaviors (Altmann 1974). Before each observation session, an individual sloth was selected at random and was the focal individual for that 24-hr sampling period. Sessions were conducted morning (0500-0800 hr) and evening (1700-2000 hr) (Sunquist and Montgomery 1973; Choi et al. 2007; Garcés-Restrepo et al. 2018). Transition times were recorded as (hh:mm:ss), indicating the time one activity stopped and another started (Chiarello et al. 2004). We characterized behavior into the following categories that represent the main states of activity in sloths: moving, feeding, resting, grooming, and alert (Chiarello et al. 2004). For each sampling period,

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Figure 2. Soft-release enclosure for rehabilitated Hoffmann’s two-toed sloths, Gamboa, Panamá, October 2019-October 2020. The soft release enclosure was a 500 m^2 outdoor area enclosed by a 1.40 m concrete wall with no additional restraints above. The enclosure had a 1.45 m high electric predator fence with 4 rows of aluminum wire mounted to plastic ground stakes.

only activity bouts that lasted ≥10 sec were recorded (Chiarello et al. 2004). To avoid observer bias, observers rotated between morning and evening sessions on a weekly basis.

Release and radiotelemetry

Two-toed sloths were removed by hand from the soft-release enclosure and transported in kennels to release sites 0.35 km – 0.55 km away in adjacent Soberania National Park. Two-toed sloths were then released onto different trees ≥300 m from one another. During March 10-October 3 2020, we used homing techniques via a Yagi 3-element antenna and a RX-0.5M receiver (Mech 1983) to obtain sloth locations and monitor survival. Locations were collected during 0700-2000 hr, 5 days/week. GPS coordinates of each two-toed sloth location were recorded using a Garmin GPSMAP 64st. When monitoring survival, the locations of dead animals were recorded, and the carcasses were collected to perform a necropsy to determine the cause of death (Whisson et al. 2012).

Habitat sampling

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We used a paired analysis approach and measured habitat variables at two-toed sloth locations and paired random locations (Compton et al. 2002; Row and Blouin-Demers 2006). At each sloth location, a nearby random location was selected and sampled based on a random bearing and a random distance from 10-25 m (Compton et al. 2002; Chiarello et al. 2004; Timm et al. 2014). The nearest tree with a dbh ≥10 cm was sampled given sloth use of trees of this size (Montgomery and Sunquist 1978; Acevedo-Quintero et al. 2011).

At sloth and random locations, we measured 8 microhabitat variables (i.e., site-level variables measured at individual trees) known to be important to habitat use by sloths (Montgomery and Sunquist 1978; Falconi et al. 2015). When a two-toed sloth was located moving on the ground towards a tree, measurements were taken at the tree eventually climbed by the sloth. Variables measured were tree species, tree height (m), height to crown base (m), diameter at breast height (dbh), abundance of lianas (%), crown width (m), crown depth (m), and canopy closure (%) (Montgomery and Sunquist 1978; Acevedo-Quintero et al. 2011; Falconi et al. 2015). Tree height, crown height, and height to crown base were measured using an optical rangefinder. Dbh was measured at 1.4 m using a diameter tape and the abundance of lianas was scaled 1 to 4, where 1 corresponded to 0-25%, 2 was 25-50%, 3 was 50-75% and 4 was 75-100% (Acevedo-Quintero et al. 2011). We measured canopy closure (%) using a spherical densitometer with readings made 20 m in all 4 cardinal directions (Strickler 1959).

Data analysis

For two-toed sloths in the soft-release enclosure, we quantified activity budgets for individual sloths using the following equation:

$$\text{min spent in each activity/ total min observation} \times 100$$

For each activity category, a linear mixed model was conducted using the using the lmer function from the "lmeTest" package (Bates et al. 2015) in R (R version 4.0.3, www.r-project.org, accessed 15 August 2020) and used to compare each two-toed sloth activity budget by sex, age, season (i.e., dry vs wet), session time (i.e., morning vs evening), and month (a=0.05 throughout). Six months were assessed (3 months per each group). The month was used as a categorical factor, and April was used as the reference category. Models were fit with Restricted Maximum Likelihood (REML) and individual sloths were treated as random effects within the model to control for pseudoreplication. A random effects one-way Analysis Of Variance (ANOVA) was carried out for each linear mixed model and fitted with Satterthwaite's approximations using the "ANOVA" function in the "lmerTest" package in R (Kuznetsova et al. 2017).

Movement trajectories of individual two-toed sloths were quantified by calculating i) mean distances (m) traveled between successive locations and ii) total linear distances (m) from the point of release to the final location obtained. Distances between successive locations were calculated using the adehabitatLT package in Program R (Calenge 2006, Version 4.0.3, R Core Team 2020), and total linear distances were calculated using ArcMap GIS version 3.0 software.

Home ranges were estimated for individuals with >20 locations (Seaman et al. 1999). Home ranges and core areas were estimated utilizing 95% and 50% fixed-kernel density methods, respectively, with bandwidth (*h*) estimated using the scaled-reference method (REF) (h_{ref}) (Worton 1989; Gitzen et al. 2006; Falconi et al. 2015). This smoothing parameter was used instead of Least Square Cross-Validation (LSCV) since two-toed sloths were frequently located in nearly identical tree locations forming clusters within home ranges (Gitzen et al. 2006). These analyses were performed using the adehabitatHR package in Program R (Calenge 2006, Version 4.0.3, R Core Team 2020).

Survival estimates for radiocollared two-toed sloths were calculated using the "survival" package in Program R (R version 4.0.3, R Core Team 2020). We estimated monthly survival rates for 30 weeks using a Kaplan-Meier survival curve with staggered entry based on date of release (Pollock et al. 1989). We also used a Kaplan-Meier survival curve to estimate survival rates using time in captivity (days) as a predictor of survival at pre-specified time intervals (300, 600, and >900 days) (Goel et al. 2010; Walker et al. 2022). Monthly survival rates were compared between sexes using the log rank test. Two-toed sloths were censored from analysis when transmitters were lost or failed and sloths with unknown fates at the end of the monitoring period were right-censored (Hosmer et al. 2008).

We calculated the mean ± SE for all habitat variables measured at sloth and random locations and used a mixed-effects conditional logistic regression model (Duchesne et al. 2010) to analyze habitat selection. All variables were examined for multicollinearity using Variance Inflation Factor (VIF) scores (Kim 2019) with highly correlated (VIF>5) variables removed from the model to avoid redundancy (Akinwande et al. 2015). Height to crown base was removed due to high collinearity with tree height, and crown width was not included due to missing values. Conditional logistic regression models were fitted using the "coxme" package in Program R (R version 4.0.3, R Core Team 2020). Individual two-toed sloths were included as a random effect to account for the lack of independence among observations. We developed 2 models: one which excluded tree species and the other which included tree species. We used an ANOVA to compare models with and without the addition of tree species. The model selection consisted of one global model when performed. Thus the global model for model 1 and model 2 retained all habitat variables.

Results

Activity budgets

We conducted 580 hr of behavioral sampling of 13 two-toed sloths (7 F, 6 M) in the soft-release enclosure during 117 days of effort. Individual activity budgets varied; however, resting was the main activity performed by two-toed sloths (Table 1). Two-toed sloths spent 80.0% of their time resting, 7.2% moving, 6.9% feeding, 4.2% alert, and 1.7% grooming.

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Month, season, and session time were the most influential predictors of activity budgets in two-toed sloths (Table 2). The month was an influential predictor of activity budgets, with sloths resting more during January and May (Table 2, p=0.03, 0.00). Moving activity budgets were most influenced by session time (Table 2), with two-toed sloths moving more during evening sessions than during morning sessions (p=0.01). Two-toed sloths also spent more time moving during the wet season than the dry season (Table 2, p=0.01) Session time influenced feeding activity budgets (Table 2), with two-toed sloths spending more time feeding in the evening than in the morning (p=0.01). Two-toed sloths were also more alert during evening sessions than during morning sessions (p=0.00).

Movements, home ranges, and survival

We analyzed movement trajectories for 10 two-toed sloths (5 M, 5 F). Mean (±SE throughout) distance traveled between successive locations was 25.6±9.5 m and mean linear distance traveled was 82.3±21.6 m. The mean number of days between successive locations was 1.8±0.1. We calculated home ranges for 7 two-toed sloths (5 M, 2 F) and collected 30.2±6.7 locations per sloth. The mean home range size was 2.92±1.19 ha with a mean core area size of 0.81±0.32 ha.

Eleven two-toed sloths (5 M, 6 F) were radio-tracked until death or loss of transmitter signal (Table 3). Two-toed sloths were radio-tracked for 210 radio-days ($\bar{x}$ per sloth = 56.6±9.9), during which we recorded 8 mortalities (5 M, 3 F). Three mortalities (1 F, 2 M) were confirmed as predation-caused; on separate occasions, cameras identified tayra (*Eira barbara*) and ocelot (*G. spp.*) as possible predators. Three sloths died from natural causes: 1 female from hemorrhaging in the intestines, kidney abnormalities, and high parasite load; 1 female from pericardial effusion and pulmonary edema; and 1 male had internal trauma, including bruising of the organs presumably sustained from falling from a tree. One female died from interspecific aggression, and one male died from unknown causes.

Monthly survival estimates for males and females were 1.00±0.00 and 0.44±0.22, respectively, and did not differ (p≤0.30). Pooled-sex monthly survival was 0.72±0.14. Sur-

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Table 1. Activity budgets for Hoffmann's two-toed sloths during soft-release, Gamboa, Colón Province, Panamá, October 2019-October 2020.

Sloth ID	Sex	Age	Resting (%)	Moving (%)	Feeding (%)	Grooming (%)	Alert (%)
S1	F	3 yr	81.5	8.5	3.4	1.6	4.8
S2	F	6 yr	86.6	5.4	3.2	1.5	3.7
S3	M	1 yr 7 mo	81.1	6.1	5.0	2.1	6.4
S4	F	1 yr 3 mo	79.7	9.1	5.8	1.1	4.3
S5	M	2 yr 2 mo	80.0	9.0	5.0	3.1	3.0
S6	F	2 yr	88.1	2.0	6.4	0.7	2.8
S7	F	1 yr	83.7	4.4	9.9	0.3	1.6
S8	M	1 yr 3 mo	73.8	8.8	12.8	1.3	3.3
S9	M	3 yr 3 mo	89.1	2.7	4.1	0.8	3.1
S10	F	1 yr	74.6	9.0	8.6	1.9	5.9
S11	M	1 yr 5 mo	71.9	10.0	13.5	1.4	3.8
S12	M	1 yr	70.5	11.0	8.3	3.8	6.4
S13	F	1 yr	78.9	8.1	4.3	3.0	5.6
Mean±SE			79.9±1.67	7.23±0.79	6.94±0.95	1.73±0.28	4.20±0.42

vival estimates for duration in captivity were 0.82±0.12 for 300 days, 0.51±0.16 for 600 days, 0.26±0.15 for 900 days, and 0.13±0.12 for ≥1800 days in captivity.

Habitat selection

We sampled habitat at 118 used and 118 random locations (Table 4). Two-toed sloths were located predominantly in mature broadleaf forest cover. We found weak evidence of

Table 2. Linear mixed models of fixed effects for Hoffmann's two-toed sloth activity budgets, Gamboa, Colón Province, Panamá, October 2019-October 2020.

Response variable	Predictor	Estimate	SE	df	T value	*Pr* (> | *z* |)
Resting	Sex M	-14.059	260.307	5.001	-0.054	0.96
	Age	5.819	6.553	2.454	0.888	0.45
	Wet season	570.229	418.801	28.591	1.362	0.18
	Dec	273.937	293.235	541.326	0.934	0.35
	Jan	717.559	332.226	545.914	2.160	0.03
	Jun	620.043	411.682	549.801	1.506	0.13
	May	1121.775	397.185	549.842	2.824	0.00
	PM session	-237.352	195.099	543.874	-1.217	0.22
Moving	Sex M	30.749	47.923	446	0.642	0.52
	Age	-0.866	1.3578	446	-0.638	0.52
	Wet season	-215.600	83.099	446	-2.594	0.01
	Dec	-11.425	74.921	446	-0.152	0.88
	Jan	-128.026	81.086	446	-1.579	0.12
	Jun	144.6528	78.2825	446	1.848	0.07
	May	137.7640	75.855	446	1.816	0.07
	PM session	-129.121	50.927	446	-2.535	0.01
Feeding	Sex M	54.980	62.643	2.461	0.878	0.46
	Age	-0.121	2.079	3.819	-0.058	0.96
	Wet season	-87.327	109.369	14.973	-0.798	0.44
	Dec	-12.798	101.654	190.011	-0.126	0.90
	Jan	-91.068	119.312	198.860	-0.763	0.45
	Jun	346.933	88.115	161.787	3.937	0.00
	May	53.398	84.409	226.559	0.633	0.53
	PM session	-195.273	77.956	105.863	-2.505	0.01
Grooming	Sex M	32.309	80.229	2.689	0.403	0.72
	Age	-1.002	2.221	1.966	-0.451	0.70
	Wet season	119.546	92.506	3.535	1.292	0.27
	Dec	45.461	41.324	189.393	1.100	0.27
	Jan	-33.906	50.334	187.434	-0.674	0.50
	Jun	-76.043	65.954	187.164	-1.153	0.25
	May	-108.962	71.517	198.977	-1.524	0.13
	PM session	-34.523	31.408	201.498	-1.099	0.27
Alert	Sex M	-9.725	52.380	7.273	-0.186	0.86
	Age	-0.752	1.392	5.586	-0.540	0.61
	Wet season	20.364	82.339	42.746	0.247	0.81
	Dec	4.222	68.524	288.130	0.062	0.95
	Jan	45.281	76.321	290.350	0.593	0.55
	Jun	106.150	80.305	289.110	1.322	0.19
	May	-83.636	79.920	272.980	-1.046	0.30
	PM session	113.412	41.945	269.948	2.704	0.00

SE, standard error; df, degrees of freedom.

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habitat selection; in both models, two-toed sloths chose trees with smaller dbh than available (Model 1, $p \leq 0.001$; Model 2, $p \leq 0.015$, Table 5). The addition of tree species was not informative ($\chi^2_{64}=79.09$, $p \leq 0.096$). Of the 46 species of trees used, two-toed sloths were most frequently located in *Luehea seemannii*, followed by *Spondias mombin* and *Guazuma ulmifolia* (Table 6).

Discussion

Activity budgets

Activity budgets of two-toed sloths in soft-release coincided with the cyclic patterns of activity for wild two-toed sloths (Sunquist and Montgomery 1973). We expected rehabilitated two-toed sloths to exhibit similar behaviors to those of wild two-toed sloths during their acclimation period in soft-release, and these expectations were met as rehabilitated two-toed sloths increased their time moving, feeding, and alert during evening observations.

Table 3. Known fates of Hoffmann's two-toed sloths, Gamboa, Colón Province, Panamá, October 2019-October 2020.

Sloth ID	Sex	Age	Fate	Cause of mortality	Date released	Last date tracked	Total days tracked
S1	F	3 yr	D	Natural	17 March 2020	26 June 2020	101
S2	F	6 yr	U		10 March 2020	14 April 2020	36
S3	M	1 yr 7 mo	D	Natural	10 March 2020	7 June 2020	90
S4	F	1 yr 3 mo	U		24 June 2020	12 July 2020	19
S5	M	2 yr 2 mo	D	Unknown	24 June 2020	28 August 2020	66
S6	F	2 yr	D	Predation	23 June 2020	16 July 2020	24
S7	F	1 yr	D	Interspecific aggression	25 June 2020	30 June 2020	5
S8	M	1 yr 3 mo	U		7 July 2020	3 September 2020	59
S9	M	3 yr 3 mo	U		23 June 2020	4 September 2020	74
S10	F	1 yr	D	Natural	24 June 2020	8 July 2020	15
S11	M	1 yr 5 mo	D	Predation	24 June 2020	5 October 2020	103

Fate outcomes during monitoring period are: U, unknown; D, died.

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Table 4. Habitat measurements for used (n=118) and random (n=118) locations used in conditional logistic regression of Hoffmann's two-toed sloths, Gamboa, Colón Province, Panamá, October 2019-October 2020.

Habitat Variable	Used		Random	
	$\bar{X}$	*SE*	$\bar{X}$	*SE*
dbh	10.1	0.6	16.0	0.6
Tree height (m)	11.4	0.5	14.0	0.4
Height to crown base (m)	6.1	0.3	7.4	0.3
Crown depth (m)	5.3	0.3	6.6	0.3
Lianas (scaled 1-4)	2.0	0.1	2.0	0.1
Canopy closure (%)	90.7	1.4	91.2	1.2

Model parameters are coded as: dbh, diameter at breast height; cd, crown depth (m); lianas, scaled 1 to 4; cc, canopy closure (%).

We also found season and month influenced activity budgets in rehabilitated two-toed sloths. During soft-release, rehabilitated two-toed sloths spent more time resting and feeding during months with higher levels of precipitation. These results likely indicate the effect of low body temperature on activity levels (Sunquist and Montgomery 1973; Milton 1990) and an increase in leaf production of new leaves for increased food availability (Milton 1990; Barone 1998).

Movements and home ranges

We expected rehabilitated two-toed sloths to travel shorter distances than wild two-toed sloths, as these individuals were captive-raised and in the process of acclimating to a new environment following their release (Berger-Tal and Saltz 2014). We found the mean distance traveled (25.6 m) of released two-toed sloths between successive locations was slightly less than the daily distance traveled of wild radiomarked two-toed sloths (38 m) on Barro Colorado Island, Panamá (Sunquist and Montgomery 1973). The relatively short distances traveled by released two-toed sloths in our study may indicate they found habitat at release sites to be adequate without the need for traveling longer distances (Stamps and Swaisgood 2007). The mean total linear distance traveled by sloths in our study (82.3 m) was also substantially less than dispersing sloths studied by Garcés-Restrepo et al. (2018) that traveled 2,957 m. We suggest individual variation and temperament likely influenced

Table 5. Conditional logistic regression model coefficients explaining habitat selection by Hoffmann's two-toed sloths, Gamboa, Colón Province, Panamá, October 2019-October 2020.

Model	coef	exp(coef)	se(coef)	z	*P*
dbh + tree height + cd + lianas + cc					
dbh	-0.133500088	0.8750274	0.03611382	-3.70	0.00
Tree height	-0.041877615	0.9589871	0.05384117	-0.78	0.44
Canopy density	0.019793359	1.0199905	0.06902323	0.29	0.77
Lianas	0.148883117	1.1605373	0.12286650	1.21	0.23
Canopy closure	-0.000912328	0.9990881	0.01189106	-0.08	0.94
Tree species + dbh + tree height + cd + lianas + cc					
Bursea simaruba	-1.59357738	1.811966e+00	2.523946e+00	-0.78	0.43
Cochlospermum vitifolium	0.59441232	1.811966e+00	2.523946e+00	0.24	0.81
Guazuma ulmifolia	-1.50625555	2.217387e-01	2.357961e+00	-0.64	0.52
Luehea seemannii	-1.83848751	1.590578e-01	2.222577e+00	-0.83	0.41
Luehea speciosa	-1.97253352	1.391040e-01	2.237110e+00	-0.88	0.38
Miconia argentea	-4.41530695	1.209084e-02	3.019364e+00	-1.46	0.14
Spondias mombin	-0.75252489	4.711754e-01	1.912419e+00	-0.39	0.69
Schefflera morototoni	-1.36311691	2.558620e-01	2.164878e+00	-0.63	0.53
Zanthoxylum setulosum	-1.17861218	3.077055e-01	2.753156e+00	-0.43	0.67
dbh	-0.22060271	8.020353e-01	9.059871e-02	-2.43	0.02
Tree height	-0.28439054	7.524727e-01	1.715414e-01	-1.66	0.10
Canopy density	0.34092777	1.406252e+00	1.814446e-01	1.88	0.06
Lianas	0.10233965	1.107760e+00	3.033484e-01	0.34	0.74
Canopy closure	0.04296174	1.043898e+00	2.703242e-02	1.59	0.11

Model coefficients are coded as: dbh, diameter at breast height; cd, canopy density (%); lianas, scaled 1 to 4; cc, canopy closure (%).

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levels of release-site fidelity and movement behaviors exhibited during this exploratory phase in rehabilitated two-toed sloths (Chiarello et al. 2004; Berger-Tal and Saltz 2014).

Mean home range size of rehabilitated two-toed sloths reported herein (<2.9 ha) is similar to findings by Montgomery and Sunquist (1978) in Central Panamá. In Costa Rica, home range sizes were 4-7.5 ha, with males occupying larger areas than females (Vaughan

Table 6. Tree species by genus used by Hoffmann's two-toed sloths, Gamboa, Colón Province, Panamá, October 2019-October 2020.

Genus	Frequency used
Luehea	34
Spondias	28
Guazuma	22
Bursera	20
Anacardium	13
Schefflera	11
Miconia	8
Cordia	8
Simarouba	5
Apeiba	5
Pittoniotis	4
Guatteria	4
Zanthoxylum	3
Chrysophyllum	2
Erythroxylum	2
Byrsonima	2
Hura	2
Trichospermum	2
Carapa	2
Garcinia	2
Laetia	2
Tabebuia	2
Cecropia	2
Maquira	2
Terminalia	2
Hasseltia	1
Tibouchina	1
Cinnamomum	1
Eugenia	1
Pysychotria	1
Astronium	1
Casearia	1
Croton	1
Roystonea	1
Beilschmiedia	1
Enterolobium	1
Ryania	1

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et al. 2007; Mendoza et al. 2015; Fountain et al. 2017). In our study, both female sloths had home ranges >3 ha, while most males had home ranges ≤1.4 ha. Observed variation in home range size between males and females likely reflect reproductive strategies of mate switching and home range shift by females, especially since both released into the wild were sexually mature (Taube et al. 2001; Garcés-Restrepo et al. 2017).

Rehabilitated two-toed sloths in our study likely occupied small home ranges as a result of either i) confinement in captivity or ii) high release-site fidelity (Stamps and Swaisgood 2007; Berger-Tal and Saltz 2014). Sloths are solitary animals that optimize energy conservation through extreme rates of decreased activity (Goffart 1971), which may imply habitats available at release sites met the biological needs of two-toed sloths (Stamps and Swaisgood 2007; Di Blanco et al. 2017). In addition to showing patterns of release-site fidelity, rehabilitated two-toed sloths may have been less inclined to establish large home ranges given the similarities between the soft-release habitat and available habitat at release sites in the wild (Bright and Morris 1994; Stamps and Swaisgood 2007).

Survival

Survival rates for rehabilitated two-toed sloths in our study (monthly estimate of 0.72) were lower than those for wild two-toed sloths. Fountain et al. (2017) found annual survival in subadult and adult two-toed sloths to be 0.92, while Peery and Pauli (2014) reported an annual survival rate of 0.90 for adults. In juveniles, Garcés-Restrepo et al. (2018) estimated annual survival at 0.88 to 1, concluding that juvenile survival was lowest immediately following maternal independence, but sufficient to maintain a stable population. Monthly survival in our study likely reflects survival during a stage comparable to the stage of maternal independence in wild conspecifics.

Survival of rehabilitated two-toed sloths in our study was likely influenced by individual temperament and duration in captivity, which affects the behavior, movement, and survival of relocated animals following release (Tribe et al. 2005; Berger-Tal and Saltz 2014; Blair et. al 2020). Survival for relocated wildlife is low in general, which can be due to duration in captivity, capture and handling stress, release techniques, naiveness, and poor habitat quality at release sites (Sarrazin and Legendre 2000; Beringer et al. 2004; Guy and Banks 2012). Of the 8 mortalities we recorded, predation and natural causes were the leading causes of mortality. Three individuals were depredated by either an ocelot or tayra, which are both agile predators found in forested areas throughout central Panamá (Moreno et al. 2006; Meyer et al. 2015). The remaining 5 mortalities included natural causes, interspecific aggression, and one unknown. The species which caused aggression that led to a sloth's mortality was unknown. Other individuals that died from natural causes may have experienced high levels of stress in addition to poor nutrition following their release. Sloths that may have experienced extreme stress and poor nutrition were likely individuals whose temperament influenced dispersal behavior (Berger-Tal and Saltz 2014). Some individuals in our study exhibited traits of boldness and increased movements during the exploratory phase, which may have resulted in increased risks of mortality (i.e., higher predation risk, energetic demands) (Berger-Tal and Saltz 2014). Other individuals avoided venturing into new areas and remained close to release sites, likely reducing exposure to hazards that may have led to mortality (McDougall et al. 2006; Watters and Meehan 2007; Berger-Tal and Saltz 2014). We found that rehabilitated sloths had a 0.51 survival estimate if kept in captivity ≤600 days, with chances of survival decreasing with increased durations in captivity (Figure 3). Many animals develop abnormal behaviors and exhibit habituation to humans following pro-

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longed care in captivity, which can decrease post-release survival as these animals lack the behaviors that contribute to overall fitness and success (Beringer et al. 2004; Hall 2005). We did not find a difference between male and female survival rates, which was likely due to small sample sizes and resulting low statistical power. However, males may have experienced higher rates of survival because females in our study traveled longer distances than males, thus presenting higher risks of overexertion, nutritional stress, dehydration, and predation (Peery and Pauli 2012, 2014).

Habitat selection

We did not find strong evidence of habitat selection in two-toed sloths. Our findings suggest that habitats available at release sites used in our study did not present much opportunity for selection, since release sites within Soberanía National Park had little heterogeneity in habitat type. The mature broadleaf forest was the dominant habitat type throughout, which provided good habitat for sloths, consisting of many trees identified as food sources with dense canopies also providing refugia and ample connectivity for movement (Montgomery and Sunquist 1978). Furthermore, sloths were likely located in trees used as daytime resting sites. Habitat sampling was conducted during daylight hours, and two-toed sloths can travel long distances during their hours of nocturnal activity, but frequently revisit what is termed their modal tree, or the tree where a sloth is located most often (Montgomery and Sunquist 1975, 1978). We observed this frequently among two-toed sloths, and this may explain the lack of evidence found for habitat selection.

We did, however, find rehabilitated two-toed sloths to use habitats similar to wild two-toed sloths, using trees with 91% canopy closure and ≥25% abundance of lianas. Acevedo-Quintero et al. (2011) reported wild two-toed sloths in Colombia used trees with canopy

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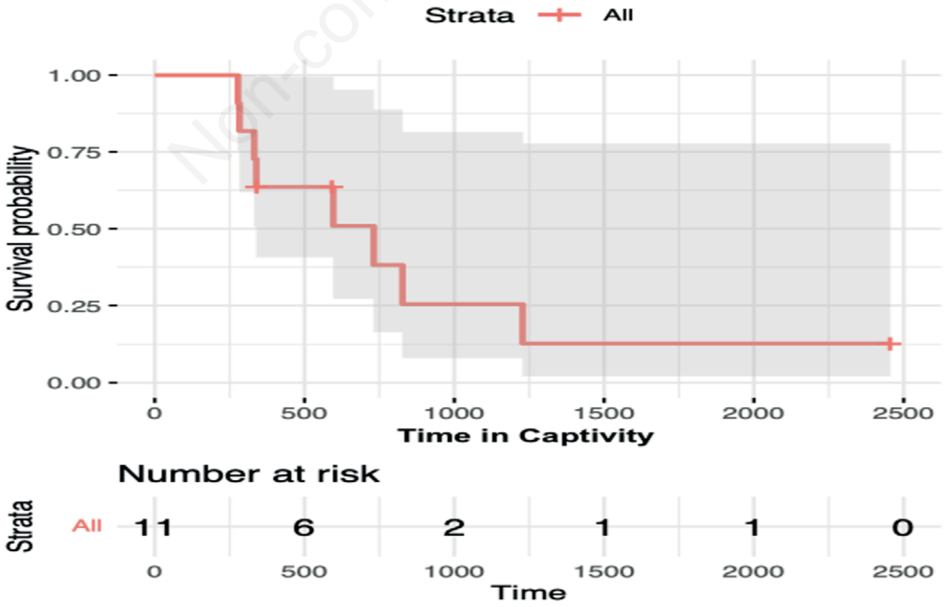

Figure 3. Survival estimates against time in captivity (days) for Hoffmann's two-toed sloths, Gamboa, Colón Province, Panamá, October 2019-October 2020.

closure between 50-100% and ≥25% abundance of lianas within the crown. These observations suggest rehabilitated two-toed sloths selected habitats which provided connectivity between large masses of lianas and dense crowns, offering daytime refugia and protection from predators (Montgomery and Sunquist 1975, 1978; Acevedo-Quintero et al. 2011). We also found rehabilitated two-toed sloths to use 46 different tree species, similar to wild two-toed sloths on Barro Colorado Island, Panamá, that used 52 tree species (Montgomery and Sunquist 1978). Of the 46 used tree species we identified, two-toed sloths were most frequently located in *L. seemannii*, *G. ulmifolia,* and *S. mombin,* which were all species provided as a food source in captivity. Two-toed sloths were fed 10 different tree species in captivity, and since food acquisition is a learned behavior in sloths, it is likely individuals were frequently located in trees they identified as a food source.

Among all habitat variables measured, dbh was the only model predictor that differed between used and random locations. Two-toed sloths may have selected trees with a smaller dbh for two reasons: i) habituation to enclosure design during captivity, or ii) as an energy-conserving mechanism. Wild two-toed sloths have been documented using trees with a dbh>15 cm (Montgomery and Sunquist 1978; Acevedo-Quintero et al. 2011), whereas we found two-toed sloths to use smaller trees. The captive pens and soft-release enclosure where rehabilitated two-toed sloths were housed prior to release included vines and thin tree branches. It is likely that two-toed sloths grew accustomed to the use of smaller trees for horizontal and vertical displacement. Alternatively, captive two-toed sloths have been observed to ascend and descend on supports of relatively small diameter (Mendel 1981). This behavior facilitates faster vertical movement, requires less energetic exertion, and allows for visual and olfactory cues to be within closer proximity to the structure that is being used (Mendel 1981). Rehabilitated sloths likely selected trees with smaller diameters, while relying on visual and olfactory senses, to become familiarized with their new environment and minimize energy expenditures (Mendel 1981).

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Conclusions

Albeit based on relatively low sample sizes and lacking a control sample of wild sloths for comparison, we obtained useful information for conservationists regarding the post-release ecology of rehabilitated and relocated two-toed sloths. Rehabilitated two-toed sloths exhibited activity patterns, movements, home range establishment, and habitat selection similar to wild two-toed sloths (Montgomery and Sunquist 1975, 1978). Differences in biology and behavior between wild two-toed sloths in other studies and rehabilitated individuals in our study were likely due to confinement. That survival was lower for rehabilitated two-toed sloths was unsurprising given all other studies have found this for reintroduced and relocated species (Sarrazin and Legendre 2000; Beringer 2004; Guy and Banks 2012). However, for an individual animal that would have likely died in the wild from habitat loss, electrocution, or an animal-vehicle collision; rescue, rehabilitation, and release back into the wild at least allows a chance at survival.

Authors' contributions

CM and CN designed the study. CM conducted the analysis and drafted the manuscript. NC and YY provided rescued sloths for this research, assisted in sloth husbandry, and assisted in performing necropsies. AC and CN revised the manuscript.

All the authors made a substantive intellectual contribution. All the authors have read and approved the final version of the manuscript and agreed to be held accountable for all aspects of the work.

Conflict of interest

The authors declare no potential conflict of interest.

Funding

This project was funded by the Cooperative Wildlife Research Laboratory, Forestry Program (via the McIntire-Stennis Cooperative Forestry Research Program), and Center for International Education at Southern Illinois University (SIU).

Availability of data and materials

All data generated or analyzed during this study are included in this published article

Acknowledgements

The Cooperative Wildlife Research Laboratory, Forestry Program, Center for International Education at Southern Illinois University (SIU) and Pan-American Conservation Association (APPC) provided funding and support for this project. We thank the staff of APPC for kindly assisting with all aspects of animal husbandry. J. Reeve, L. Park, and S. Anile at SIU provided logistical support. M. Rivas, A. Sanchez, and R. Cruz of APPC provided data collection and field assistance.

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