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Of lemurs and louse flies: The biogeochemical and biotic effects of forest disturbance on *Propithecus edwardsi* and its obligate ectoparasite *Allobosca crassipes* in Ranomafana National Park, southeastern Madagascar

Elizabeth McGee[1] | **Stanley Vaughn**[2]

[1] Department of Biological Sciences, San José State University, San Jose, California

[2] College of Science, San José State University, San Jose, California

Correspondence
Elizabeth McGee, Department of Biological Sciences, San Jose State University, San Jose, CA 95192-0100.
Email: elizabeth.mcgee@sjsu.edu

From alleles to ecosystems and landscapes, anthropogenic activity continues to affect the environment, with particularly adverse effects on biodiversity hotspots such as Madagascar. Selective logging has been proposed as a "win-win" conservation strategy, yet its effects on different components of biodiversity are still not fully understood. Here we examine biotic factors (i.e., dietary differences) that may be driving differences in biogeochemical stocks between disturbed and undisturbed forests. We present the stable nitrogen ($\delta^{15}N$) and carbon ($\delta^{13}C$) isotope composition of hair from the lemur *Propithecus edwardsi* and of whole bodies of its obligate ectoparasite, the louse-fly *Allobosca crassipes*, from sites in Ranomafana National Park (RNP) that are comparable except for the history of logging and subsequent forest regeneration. *P. edwardsi* and *A. crassipes* from the disturbed (i.e., heavily selectively logged) site are lower in ^{15}N and ^{13}C relative to *P. edwardsi* and *A. crassipes* from sites that were minimally selectively logged or not commercially logged at all. There is a ~3‰ decrease in ^{15}N between disturbed and undisturbed sites that corresponds to a difference of nearly a full trophic level. Flowers from *Bakerella clavata*, a staple food source for *P. edwardsi* in disturbed habitats and a fallback food for *P. edwardsi* in primary forests, were also analyzed isotopically. *B. clavata* is $\delta^{15}N$-depleted in both disturbed and undisturbed sites. Data from longitudinal behavioral surveys of *P. edwardsi* in RNP and other forests in eastern Madagascar point to significant differences in consumption patterns of *B. clavata*, with *P. edwardsi* in disturbed forests consuming almost twice as much of this plant. Depletion of ^{15}N in animal tissues is a complex issue, but likely the result of the interaction of physiological and ecological factors. Anthropogenic disturbance in RNP from selective logging has had both biotic and biogeochemical effects that are observable trophically.

KEYWORDS
Allobosca crassipes, biogeochemical effects, biotic effects, *Propithecus edwardsi*, selective logging

1 | INTRODUCTION

Habitat destruction is considered one of the greatest threats to some 634 primate species, nearly half of which (48%) are on the IUCN Red List of Threatened Species (www.iucnredlist.org/search Primates). Madagascar primates are of particular interest because of the exceptionally high rate of endemism, isolation, and habitat destruction that characterizes this island (Mittermeier et al., 2008). The effect of

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isolation on this island's fauna and flora for over 88 million years (Krause, 2003) is evident in the documented 2,463 non-marine plants, 4,976 non-marine invertebrate species, and 739 land vertebrates (including ~100 species of lemurs) that are endemic to the island (Goodman & Benstead, 2005; Mittermeier et al., 2008). When considering the numbers of endemic flora and fauna and habitat loss, Madagascar ranks as one of the "hottest" of the world's biodiversity hotspots (Myers, Mittermeier, Mittermeier, da Fonseca, & Kent, 2000).

Selective logging or sustainable timber management has been suggested as a necessary compromise that balances the demand for timber products with the critical need to protect biodiversity (Pearce, Putz, & Vanclay, 2003; Whitmore, 1999). Such compromises, however, hinge on an integrated understanding of how logging affects biodiversity (Redford & Richter, 1999). It is useful to consider the impact of logging on biodiversity by first disaggregating biodiversity into its different components and their attributes. Floral tropical forest biodiversity includes genetic, species/population, community, ecosystem, and landscape components (Putz, Blate, Redford, Fimbel, & Robinson, 2001, after Redford & Richter, 1999). Each biodiversity component has attributes that define its structure (i.e., physical organization or pattern), composition (i.e., identity and variety), and function (i.e., ecological and evolutionary processes). Faunal biodiversity may similarly be disaggregated to understand the impact of logging, with many of the same components and attributes used by Putz et al. (2001) (Fig. 1).

The impact of logging on the eastern rainforests of Madagascar is of concern given that less than one-third of the original forest cover remains (Green & Sussman, 1990). The establishment of the Institute for the Conservation of Tropical Environments by Wright led to collaborations and exchanges among scientists resulting in over 800 publications from 1987 to 2016. Of the nearly 100 publications that focus on the effects of logging or habitat modification in the rainforests of eastern Madagascar, the majority address compositional or functional change at the species or population level (e.g., Crowley et al., 2011; Crowley, Blanco, Arrigo-Nelson, & Irwin, 2013; Gerber, Arrigo-Nelson, Karpanty, Kotschwar, & Wright, 2012; Herrera, Wright, Lauterbur, Ratovonjanahary, & Taylor, 2011; Irwin et al., 2010; Pochron, Tucker, & Wright, 2004; Wright, 1995). Research on the effects of logging on composition or function at the community level comprises ~20% of the total (e.g., Benstead, Douglas, & Pringle, 2003; Bixby, Benstead, Douglas, & Pringle, 2009; Brown & Gurevitch, 2004; Bublitz et al., 2015; Rainio & Niemelä, 2006; Razafindratsima, Jones, & Dunham, 2014; Wright et al., 2011), while research on the effects of logging on structural/compositional and functional attributes of the genetic component of biodiversity accounts for ~10% of the total (e.g., Baden et al., 2014; Tomiuk et al., 1998; Yoder et al., 2000). Within the last 15 years, the scope of research on the effects of logging and habitat disturbance has expanded to examine the impact on compositional and/or functional biodiversity at the species or

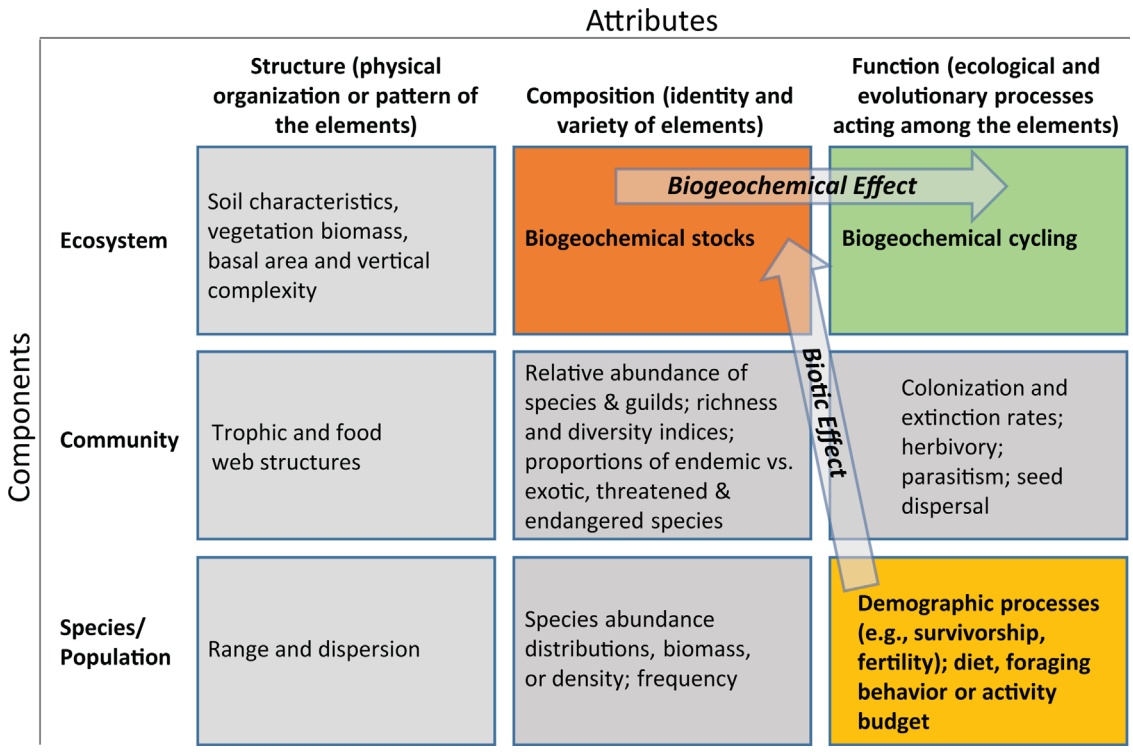

FIGURE 1 Effects of logging on three components of biodiversity (species/populations, community, and ecosystem) and respective attributes (structural, compositional, and functional). This paper focuses on biotic effects in *P. edwardsi* due to behavioral adaptations in diet, and the biogeochemical effects within a single trophic level and one step above in *A. crassipes*. Adapted from Putz et al. (2001)

population level within the context of landscape, particularly with respect to habitat patches and edge effects (e.g., Brown, Parks, Bethell, Johnson, & Mulligan, 2015; Holmes et al., 2013; Lehtonen, Mustonen, Ramiarinjanahary, Niemelä, & Rita, 2001; Lehman, Rajaonson, & Day, 2006a; Lehman, Rajaonson, & Day, 2006b; Irwin, 2007, 2008a, 2008b; Irwin, Raharison, & Wright, 2009).

Research on the ecosystem-level effects of logging in eastern Madagascar has been less extensive and has typically focused on structural attributes such as soil characteristics (e.g., Styger, Rakotondramasy, Pfeffer, Fernandes, & Bates, 2007) or functional attributes including watershed and nutrient cycling (e.g., Brand & Pfund, 1998; Kramer, Richter, Pattanayak, & Sharma, 1997) or ecosystem services (e.g., Kari & Korhonen-Kurki, 2013). Here we consider the compositional and functional effects of selective logging on a tropical rainforest ecosystem in Ranomafana National Park in southeastern Madagascar. Specifically, that habitat modification due to selective logging alters biogeochemical stocks (i.e., a compositional attribute), which in turn affect biogeochemical cycling (i.e., a functional attribute) (Fig. 1).

Ranomafana National Park (RNP; 47° 18'–47° 37E, 21°02'–21°25 S; Fig. 2) is exceptionally high in primate diversity with 13 species of lemurs. RNP is in a low to high montane rainforest that ranges in elevation from 600 to 1,500 m. (Wright, 1992, 1995). The dry season occurs from June to August (average temperature 10–16°C), and the wet season is January and February (average temperature 17–25°C) (Centre ValBio, unpublished data). Prior to the establishment of RNP in the early-1990s, approximately one third of the park's 43,500 hectares had been affected by selective logging between 1987 and 1991 (Dew & Wright, 1998; Wright, 1992, 1997). Historically, logging represents the most frequent anthropogenic disturbance within and around RNP.

We examine stable carbon (^{13}C) and stable nitrogen (^{15}N) isotopes in Milne Edwards sifaka (*Propithecus edwardsi*) and an obligate ectoparasite of this lemur, the louse fly *Allobosca crassipes*, to understand the biotic and biogeochemical effects of habitat degradation in RNP. We hypothesize that ^{15}N and ^{13}C will be significantly lower in *P. edwardsi* inhabiting disturbed versus undisturbed forests in RNP that are largely comparable except for forest disturbance. We also

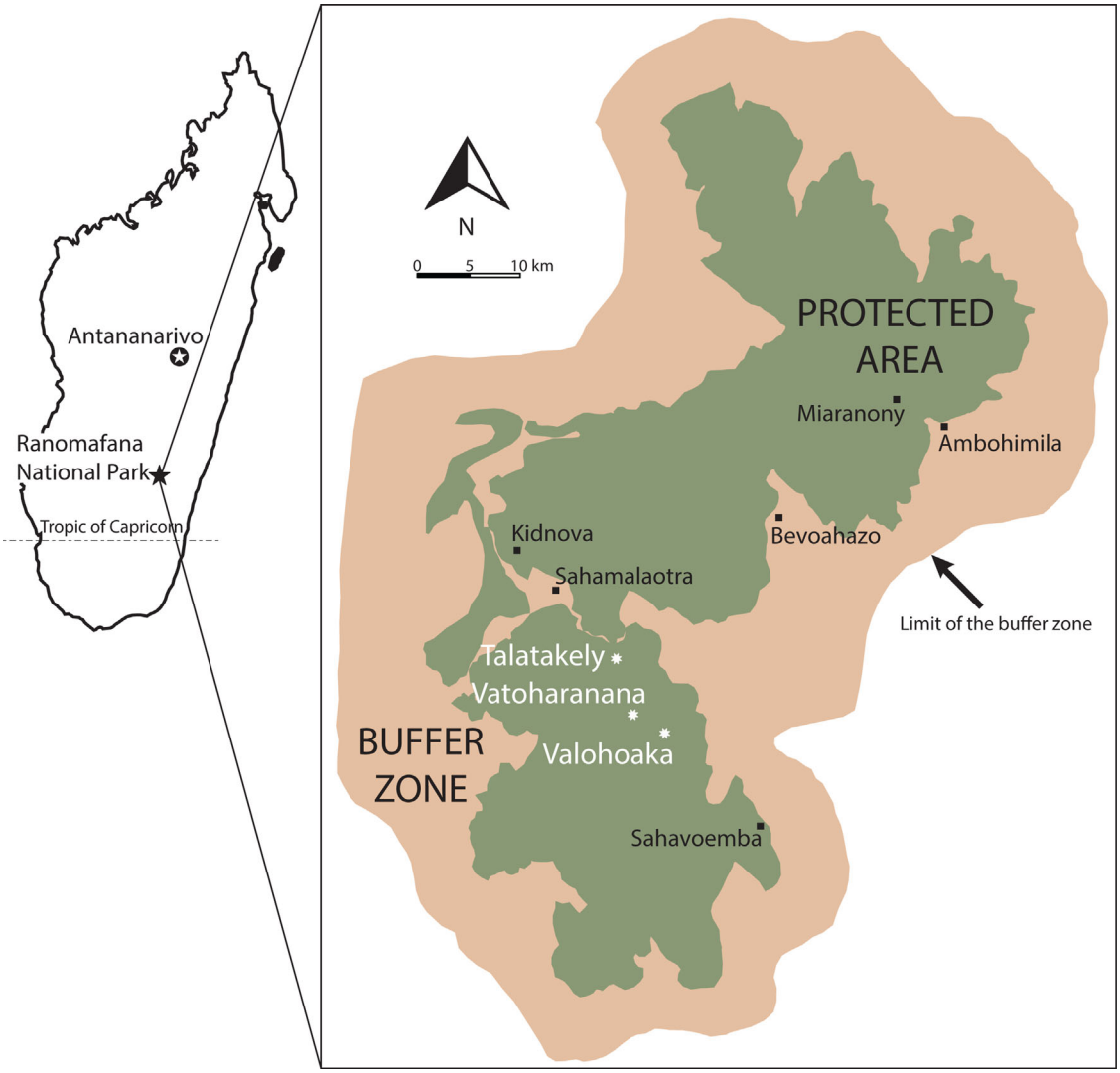

FIGURE 2 Location of Ranomafana National Park in southeastern Madagascar. Enlarged map shows the location of the study sites of Talatakely, Vatoharanana, and Valohoaka

predict lower ^{15}N and ^{13}C in *A. crassipes*, that is, in organisms at the next trophic step. We examine biotic factors (i.e., dietary differences) in *P. edwardsi* populations in RNP that may be driving differences in biogeochemical stocks between disturbed and undisturbed forests within Ranomafana (i.e., a functional attribute at the species/population level; Fig. 1).

1.1 | Stable isotope ecology in brief

Several elements occur as stable isotopes (i.e., atoms of the same element with different numbers of neutrons); a few of the ecologically interesting stable isotopes include sulfur (^{34}S), nitrogen (^{15}N), carbon (^{13}C), and oxygen (^{18}O) (Ehleringer & Rundel, 1989). As these isotopes move through their respective biogeochemical cycles, plants and animals incorporate the isotopes into their tissues, with predictable offsets, or fractionations, from the isotope values of source of the isotope (e.g., plants ingested by an animal). Therefore, an organism's diet directly determines its isotopic composition and indirectly provides information about energy transfer in an ecosystem.

Natural variations in stable carbon isotopes of plants are the result of physiological processes and environmental conditions which have been used to infer, among other things, diet, and habitat preferences. Differences in $\delta^{13}C$ have been the basis for many studies aimed at identifying or reconstructing diet preferences in herbivorous mammals (e.g., Ambrose & DeNiro, 1986; Codron, Lee-Thorp, Sponheimer, de Ruiter, & Codron, 2006; Crowley et al., 2010; DeNiro & Epstein, 1978, 1981; Loudon, Sponheimer, Sauther, & Cuozzo, 2007; Loudon, Sandberg, Wrangham, Fahey, & Sponheimer, 2016; Minson, Ludlow, & Troughton, 1975; O'Regan et al., 2008; Schoeninger, Iwaniec, & Glander, 1997; Schoeninger, Iwaniec, & Nash, 1998; Schoeninger, Moore, & Sept, 1999; Smith, Morgan, & Pilbeam, 2010; Sponheimer et al., 2003). Differences in photosynthetic pathways of C_3, C_4, and CAM plants result in fractionation differences, with C_3 and C_4 plants having average $\delta^{13}C$ values of −27‰ and −13‰, respectively (Koch, 2007). CAM plants have $\delta^{13}C$ values that are intermediate between C_3 and C_4 plants (O'Leary, 1988). Stable isotope variations in C_3 plants have been of particular interest in primatology, given that many primate species inhabit biomes where C_3 woody trees and shrubs are the dominant vegetation. The presence of a vertical cline (the "canopy effect") in ^{13}C in leaves from the forest floor to the top of the canopy has been noted in forests (Medina & Minchin, 1980; Medina, Sternberg, & Cuevas, 1991; van der Merwe & Medina, 1989; but see Blumenthal, Rothman, Chritz, & Cerling, 2016). Vegetation nearest the floor is noticeably more ^{13}C-depleted than the ^{13}C of vegetation further up in the canopy. Accordingly, stable carbon isotopes have also been used to determine whether C_3 consumers feed on/near the forest floor or in the canopy (e.g., Ambrose & DeNiro, 1986, 1989; Cerling, Hart, & Hart, 2004; Krigbaum, Berger, Daegling, & McGraw, 2013; Schoeninger et al., 1998, 1999). Thus, in a forest ecosystem, $\delta^{13}C$ can be an indicator of habitat exploitation. Other factors affecting variations in ^{13}C, including water availability, temperature, and light, are reviewed by Crowley (2012), Sandberg, Loudon, & Sponheimer, 2012, and Blumenthal et al. (2016).

Stable nitrogen isotope composition can be used as an indicator of trophic level (e.g., plant to herbivore to carnivore) in terrestrial ecosystems, with each step characterized isotopically by an average 3‰ enrichment in $\delta^{15}N$ (DeNiro & Epstein, 1981; Ehleringer & Cerling, 2002; Schoeninger & DeNiro, 1984; Schoeninger, Most, Moore, & Somerville, 2016). Causes of natural variations in stable nitrogen isotopes in plants are complex and involve a variety of factors, including nitrogen availability, fixation, and heterogeneity of ^{15}N in the plant itself, temperature, and precipitation (Amundson et al., 2003; Marshall, Brooks, & Lajtha, 2007). Some general but very useful patterns have been observed, however. In terrestrial systems, nitrogen-fixing plants (e.g., legumes) are ^{15}N-depleted compared to non-nitrogen-fixing plants due to differences in nitrogen sources, that is, nitrogen-fixing bacteria embedded in the roots of the plant (e.g., legumes) or the soil (Schmidt & Stewart, 2003; Stewart, 2001; but see Marshall et al., 2007). Animals consuming legumes in turn may be depleted in ^{15}N according to relative use of legumes in the diet (Ambrose & DeNiro, 1986; Schoeninger et al., 1998). A correlation also exists between ^{15}N in soil and plants, and climate. Increased mean annual precipitation and decreased mean annual temperature results in lower ^{15}N values both locally and globally (Amundson et al., 2003; Austin & Vitousek, 1998; Heaton, Vogel, von la Chevallerie, & Collett, 1986). These patterns are also observed in consumers, for example, drought-tolerant herbivores are $\delta^{15}N$-enriched (Ambrose & DeNiro, 1986; Heaton et al., 1986; but see Cormie & Schwarcz, 1996 and Schoeninger et al., 2016). Additional background on variables affecting ^{15}N in animals and their food webs is provided in Ambrose (1991), Kelly (2000), and Robbins, Felicetti, and Florin (2010).

This research complied with the laws of Madagascar for biological field research and was authorized by the Madagascar National Parks, the Commission Ad Hoc Flore et Faune du Comité d'Orientation de la Recherche Environnementale (CAFF/CORE), and the Madagascar Ministry of the Environment, and was approved by San Jose State University's Institutional Animal Care and Use Committee (IACUC; Protocol #728). This research adhered to the American Society of Primatologists principles for the ethical treatment of primates.

2 | METHODS

2.1 | Study species

Milne Edwards' sifakas, *P. edwardsi*, and the louse fly, *A. crassipes*, are found together at several sites within ~10 km from each other in RNP that vary in degree of anthropogenic disturbance. Sifakas (*Propithecus*) are highly adept arboreal, medium-sized (~5–6 kg), sexually monomorphic primates endemic to Madagascar (Arrigo-Nelson, 2006; Pochron et al., 2004; Wright, 1995). The geographic range of *P. edwardsi* is restricted to a narrow north-south transect of low to mid-elevation montane cloud and rainforests between Mangoro/Onive Rivers to the north and Manampatrana River to the south (in total, ~5,170 km^2) (Irwin, Johnson, & Wright, 2005).

Like all sifakas, *P. edwardsi* is an anatomical folivore, but will feed on fruits and seeds when available (Arrigo-Nelson, 2006; Hemingway, 1998). *P. edwardsi* has also been observed ingesting soil and small quantities of insect larvae on occasion (Arrigo-Nelson, Baden, Salisbury, Wright, & McGee, 2010). *P. edwardsi* is ideal for this analysis for several reasons. It is an anatomical folivore whose feeding behavior and habitat use has been well-studied for over 25 years (Pochron et al., 2004). All animals 2 years or older are collared and therefore identifiable. *P. edwardsi* is also present in both disturbed and undisturbed areas within RNP.

The louse fly *A. crassipes* (Fig. 3) is the monotypic representative of *Allobosca* (*Hippoboscidae*: *Diptera*), and is endemic to Madagascar (Maa, 1969). Flies of the family *Hippoboscidae*, commonly known as louse flies, are obligate ectoparasites of birds and mammals, including lemurs (Maa, 1969; Vaughn & McGee, 2009). This family comprises over 200 species, with 21 genera divided into 3 subfamilies. These flies are patchily distributed, with locality records world-wide except from the polar regions (Maa, 1969). Hippoboscids exhibit an unusual reproductive strategy with respect to most Diptera in that the females do not lay eggs. Instead, the females hold the larvae in their abdomen until they develop as pupae which are then deposited on the substrate, in proximity of or on the host (Bequaert, 1953). Although many louse flies are excellent fliers, others have vestigial wings that render them flightless (Ferris & Cole, 1922). *A. crassipes* most likely emerges with functional wings but then loses the basal portion of the wings soon after acquiring a host (Theodor & Oldroyd, 1965). All *A. crassipes* specimens collected from lemurs in RNP exhibited wing reduction (i.e., were flightless). Once *A. crassipes* reaches a host, it is likely that it remains on this host for the remainder of its life.

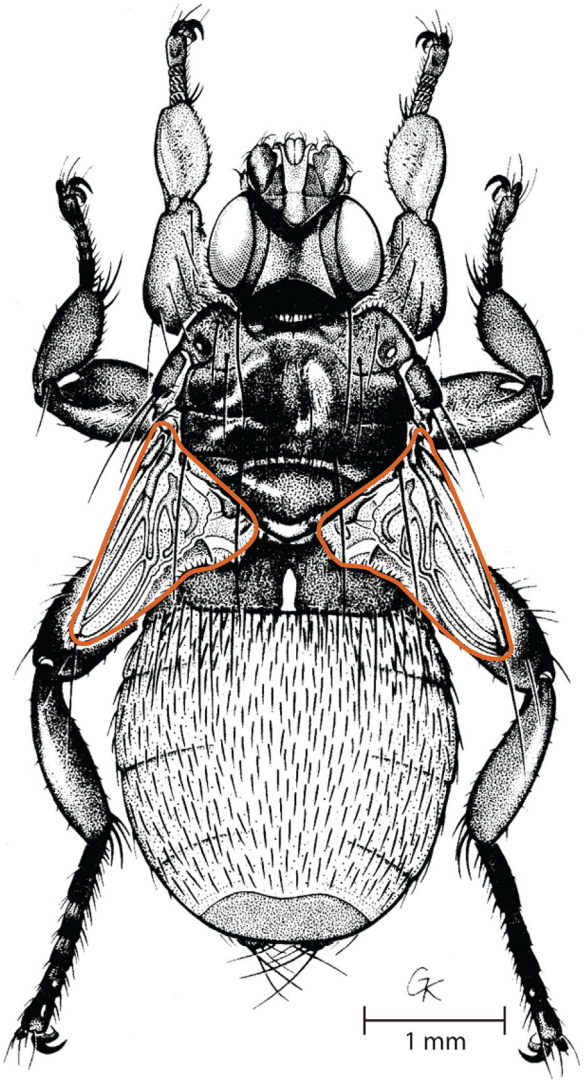

FIGURE 3 *Allobosca crassipes*, male, dorsal view. Specimen shows reduced wings (outlined in orange). Once acquiring a host, *A. crassipes* sheds the basal portion of the wing, rendering the fly flightless

2.2 | Study sites

Three collection sites were targeted for this study, all of which are located in the southern half of RNP and accessed via a trail system used by researchers and tourists (Fig. 1, Table 1). Talatakely (elevation 900 m) is located near the park entrance, and has the longest history of human impact. A small village (<50 people) was located in the vicinity of Talatakely in the 1930s and 1940s. From 1986 to 1989, timber concessions were granted access to selectively log the area. An international research station overseen by Madagascar National Parks (MNP) and the Madagascar Institut pour la Conservation des Ecosystems Tropicaux (MICET) was located in Talatakely from 1986 to 2002. In 2003, the research station was moved to a location (Centre ValBio) just outside the park entrance. Talatakely encompasses ~3 km^2 of a mixed primary/secondary forest (Balko & Underwood, 2005).

The other two sites have been impacted considerably less by anthropogenic activity. Vatoharanana, which is ~6 km southeast of Talatakely and at a slightly higher elevation (1,100–1,200 m), was minimally selectively logged from 1988 to 1989. It encompasses ~8 km^2, and is considered a primary forest today. Vatoharanana has had two satellite camps. The first operated from 1988 to 2005 for researchers and students. In 2005, MNP constructed a basic camp site for short-term stays by tourists, as well as for researchers operating out of Centre ValBio. Valohoaka is further to the southeast about 8.5 km from Talatakely and at an elevation of 1,200 m. It encompasses ~9 km^2 of primary/old growth vegetation and has not been commercially logged. A small satellite research camp has been located at Valohoaka since 1990.

2.3 | Sampling

2.3.1 | Sifakas

Hair was sampled from *P. edwardsi* at Talatakely (34 individuals), Vatoharanana (13 individuals), and Valohoaka (13 individuals) between 2000 and 2005. Animals were darted using the Pneu–Dart system, a carbon dioxide-powered gun containing disposable nonbarbed darts loaded with Telazol (20 mg/kg, after Glander, Wright, Daniels, &

TABLE 1 Forest characteristics and anthropogenic disturbance history in RNP by site

	Talatakely	Vatoharanana	Valohoaka
Elevation (m)[c]	934	1025	827–1215
Mean tree height (m)[b]	13.22	15.07	14.82
Mean tree DBH (cm)[b]	19.76	31.20	29.38
Mean crown volume (m^3)[a]	198.52	238.73	259.47
Forest type	Mixed primary/secondary	Primary	Primary
Anthropogenic disturbance	Inhabited 1930s–1940s; heavily selectively logged 1986-1990; Research station 1986–2002.	Minimal selective logging 1988–1989; satellite research camp 1988–2005; ANGAP satellite camp 2005-present.	Not commercially logged; satellite research camp 1990 to present.

[a]Balko (1998), [b]Balko and Underwood (2005), [c]Wright et al. (2008).

Merenlender, 1992). Once the animal was sedated, a small amount of hair (~5 mg) was clipped from the sacrum-tail juncture using clean scissors. As each individual was identifiable by a collar system maintained by Centre ValBio, it was easy to determine the identity and history of each sifaka. Our team worked in tandem with other researchers during darting operations so that data from different studies (e.g., genetic, morphometric, health status, etc.) could be obtained from each anesthetized animal in a single session.

2.3.2 | Louse flies

Live specimens of *A. crassipes* were collected from *P. edwardsi* in Talatakely, Vatoharanana, and Valohoaka at the same time that hair was obtained from the sifakas during the 2000–2001 field seasons. Fly specimens ($n = 101$) were collected within 30 min of capture of the hosts using forceps and a flea comb, and preserved in 80% ETOH. Precautions to prevent contamination by louse flies from different hosts included separation and isolation of sifakas prior to and during collection, and cleaning and disinfecting all examination tables. Of the 101 flies collected, 5 and 7 were selected from Talatakely and Vatoharanana, respectively, for isotope analysis. Because the sample size of flies collected from Valohoaka is small ($n = 4$ from a total of two sifikas), we chose to reserve these specimens for future systematic or taxonomic study.

2.3.3 | Plant collection

As part of a general botanical survey in 2003 and 2006, we collected 6 and 10 specimens of flowers from *Bakerella clavata* from Valohoaka and Talatakely, respectively. (*B. clavata* is present at Vatoharanana, but we did not obtain samples during our survey.) Plants were wrapped in foil and dried at 40°C for approximately 3 days immediately following collection.

2.4 | Stable isotope analysis

Sifaka hair was rinsed in a chloroform/methanol solution to remove lipids, air dried, and loaded into tin capsules in ~1 mg quantities. Select flies from each of the three sites were dried, crushed in entirety and placed into tin capsules. Dry sample weights for the flies ranged from 0.900 to 1.300 mg. Plants were freeze dried and crushed, and ~2 mg samples were loaded into tin capsules. All samples were then combusted in an elemental analyzer, after which stable isotopes abundances were determined using a flow-through inlet system on a continuous-flow isotope-ratio mass spectrometer (IRM; Finnigan, Bremen, Germany) at the University of Utah's Stable Isotope Research for Environmental Research (SIRFER) lab. Samples were analyzed at SIRFER over seven analytical runs between 2000 and 2010, each of which used standards (i.e., yeast and glutamic acids) repeated 2–5 times throughout the runs. For the sifaka hair, the standard deviation for replicate measures of a yeast standard for samples analyzed in 2000, 2001, 2003, and 2006 was ≤0.1‰ for $\delta^{13}C$ and $\delta^{15}N$. Sifaka hair analyzed in 2002 had a standard deviation for replicate measures of the same reference material of 0.0‰ for $\delta^{13}C$ and 0.2‰ for $\delta^{15}N$. For *B. clavata* samples analyzed in 2007, the standard deviation for replicate measures of laboratory reference materials (glutamic acids calibrated against USGS 40 and USGS 41) was ≤0.07‰ for $\delta^{13}C$ and $\delta^{15}N$. For the flies analyzed in 2010, the standard deviation for replicate measures of the same reference materials was ≤0.1‰ for $\delta^{13}C$ and $\delta^{15}N$. We use delta notation to report stable isotope ratios (heavy to light) in parts per thousand (‰) of a sample relative to a standard, where $\delta = ([R_{sample}/R_{standard}]-1) * 1{,}000$. $R = {}^{13}C/{}^{12}C$ or ${}^{15}N/{}^{14}N$. The standard for nitrogen is atmospheric air, and the standard for carbon is the Peedee belemnite marine limestone (Ehleringer & Rundel, 1989).

2.5 | Data analysis

To determine whether parametric analysis was appropriate for carbon and nitrogen isotope data for *P. edwardsi*, *A. crassipes*, and *B. clavata*, we used the Shapiro–Wilk test for normality and Levene's statistic for test of homogeneity of variances. To test for differences in isotope composition in *P. edwardsi*, *A. crassipes*, and *B. clavata* due to locality (i.e., Talatakely, Vatoharanana, and Valohoaka), we used the General Linear Model (GLM) function in SPSS (Ver. 22) to perform an ANOVA

as well as effect size analysis. We also used the GLM to test for seasonal differences in isotope composition in 2000 where we were collected hair from the many of the same individuals of *P. edwardsi* in austral spring and austral fall. Hochberg's GT2 post hoc test (Field, 2009) was used to determine where pairwise differences between sites occurred in isotope composition in *P. edwardsi*. A hierarchical cluster analysis using average linkage between groups was also used to determine whether the isotopic composition of *P. edwardsi* was clustered according to (i) disturbed (Talatakely) versus non-disturbed sites (Vatoharanana and Valohoaka); and (ii) season of collection for Talatakely.

3 | RESULTS

Stable carbon composition ($\delta^{13}C$) in *P. edwardsi* collected during different seasons in 2000 ($n = 9$ and $n = 12$ for austral fall and austral spring, respectively) at Talatakely was not significantly different ($F(1,19) = 2.722$, $p = 0.115$). Similarly, $\delta^{15}N$ was not significantly different ($F(1,19) = 0.474$, $p = 0.500$). Levene's test of homogeneity of variance indicates that variance in $\delta^{13}C$ and $\delta^{15}N$ of *P. edwardsi* hair samples from austral fall and austral spring is homogenous ($p = 0.234$ and $p = 0.738$, respectively). Hierarchical cluster analysis of these data likewise failed to distinguish between austral fall and austral spring. The lack of seasonal distinction in isotope composition was instrumental in determining our research schedule, with all subsequent collection efforts occurring in austral spring in Madagascar.

Descriptive statistics for $\delta^{13}C$ and $\delta^{15}N$ for *P. edwardsi*, *A. crassipes*, and *B. clavata* by site are reported in Table 2. In all but one case, $\delta^{13}C$ and $\delta^{15}N$ are lighter at Talatakely than at Vatoharanana and/or Valohoaka. The mean for $\delta^{13}C$ of *P. edwardsi* is about 0.5‰ lighter at Talatakely ($\bar{x} = -23.451 \pm SD$ 0.235‰) than Vatoharanana ($\bar{x} = -22.967 \pm SD$ 0.148‰) and Valohoaka ($\bar{x} = -22.933 \pm SD$ 0.212‰). The mean for $\delta^{15}N$ of *P. edwardsi* is about 1‰ lighter at Talatakely ($\bar{x} = 2.264 \pm SD$ 0.333‰) than Vatoharanana ($\bar{x} = 3.300 \pm SD$ 0.274‰) and Valohoaka ($\bar{x} = 3.222 \pm SD$ 0.211‰). The mean for $\delta^{13}C$ of *A. crassipes* is comparable between Talatakely ($\bar{x} = -24.780 \pm SD$ 0.657‰) and Vatoharanana ($\bar{x} = -24.500 \pm SD$ 0.238‰). The mean for $\delta^{15}N$ of *A. crassipes* is ~1‰ lighter at Talatakely ($\bar{x} = 8.020 \pm SD$ 0.455‰) than Vatoharanana ($\bar{x} = 9.014 \pm SD$ 0.367‰). For *B. clavata*, the mean for $\delta^{13}C$ is ~0.5‰ lighter at Talatakely ($\bar{x} = -29.870 \pm SD$ 1.815‰) than at Valohoaka ($\bar{x} = -28.883 \pm SD$ 1.242‰), whereas the mean for $\delta^{15}N$ is more than 1‰ lighter at Talatakely ($\bar{x} = -1.5 \pm SD$ 2.087‰) than at Valohoaka ($\bar{x} = 0.267 \pm SD$ 0.198‰). In all comparisons, Levene's test of homogeneity of variance indicates that variance in $\delta^{13}C$ and $\delta^{15}N$ is homogenous.

We found that $\delta^{13}C$ for *P. edwardsi* was significantly different among all 3 sites (ANOVA: $F = 35.877$, df = 2, $p < 0.001$, $\eta = 0.575$). Likewise, $\delta^{15}N$ for *P. edwardsi* was significantly different among all three sites (ANOVA: $F = 72.817$, df = 2, $p < 0.001$, $\eta = 0.733$). From η (a measure of effect size) we see that 57.5% of the variance in $\delta^{13}C$ is accounted for by site, while 73.3% of the variance in $\delta^{15}N$ is accounted for by site.

Post hoc analysis of $\delta^{13}C$ indicated a significant difference between carbon isotope composition between Talatakely and Vatoharanana (Hochberg's GT2 test, $p < 0.001$), and Talatakely and Valohoaka (Hochberg's GT2 test, $p < 0.001$), but not between Vatoharanana and Valohoaka (Hochberg's GT2 test, $p = 0.978$). Post hoc analysis of $\delta^{15}N$ indicated a significant difference in $\delta^{15}N$ between Talatakely and Vatoharanana (Hochberg's GT2 test, $p < 0.001$), and Talatakely and Valohoaka (Hochberg's GT2 test, $p < 0.001$), but not between Vatoharanana and Valohoaka (Hochberg's GT2 test, $p = 0.912$).

Cluster analysis using $\delta^{13}C$ and $\delta^{15}N$ as variables against site showed a deep bifurcation between *P. edwardsi* from Vatoharanana and Valohoaka and *P. edwardsi* from Talatakely. This clustering was also evident in a basic plot of $\delta^{15}N$ against $\delta^{13}C$ in *P. edwardsi* in disturbed versus undisturbed forests (Fig. 4).

With respect to *A. crassipes*, $\delta^{15}N$ is significantly different between Talatakely and Vatoharanana (ANOVA: $F = 17.619$, df = 1, $p < 0.01$, $\eta = 0.638$), and 63.8% of the variance in stable nitrogen composition is

TABLE 2 Stable isotope composition in *P. edwardsi*, *A. crassipes*, and *B. clavata* by site in RNP

		$\delta^{15}N$ (AIR) (‰)		$\delta^{13}C$ (PDB) (‰)	
	n	Mean	Standard deviation	Mean	Standard deviation
Talatakely					
P. edwardsi	34	2.264	0.333	−23.451	0.235
A. crassipes	5	8.020	0.455	−24.780	0.657
B. clavata	10	−1.5	2.087	−29.870	1.815
Vatoharanana					
P. edwardsi	13	3.300	0.274	−22.967	0.148
A. crassipes	7	9.014	0.367	−24.500	0.238
Valohoaka					
P. edwardsi	9	3.222	0.211	−22.933	0.212
B. clavata	6	0.267	0.198	−28.883	1.242

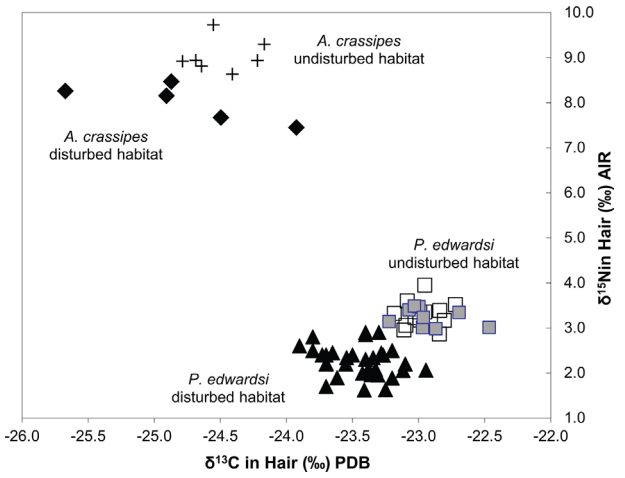

FIGURE 4 Biogeochemical profile of the sifaka *P. edwardsi* and its obligate ectoparasite, *A. crassipes*, from disturbed (i.e., Talatakely) and undisturbed (i.e., Vatoharanana and Valohoaka) forests in Ranomafana National Park. *A. crassipes* is denoted by filled diamonds in Talatakely and crosses in Vatoharanana. *P. edwardsi* is denoted by filled triangles in Talatakely, open squares in Vatoharanana and closed squares in Valohoaka. Isotope composition for *P. edwardsi* in Vatoharanana and Valohoaka is statistically indistinguishable

accounted for by site. Composition of $\delta^{13}C$ for *A. crassipes*, however, was not significantly different between Talatakely and Vatoharanana (ANOVA: $F = 1.106$, df = 1, $p = 0.318$, $\eta = 0.100$).

Stable isotope composition for *B. clavata* did not vary statistically between Talatakely and Valohoaka for either $\delta^{13}C$ (ANOVA: $F = 1.368$, df = 1, $p = 0.262$, $\eta = 0.089$) or $\delta^{15}N$ (ANOVA: $F = 2.787$, df = 1, $p = 0.117$, $\eta = 0.166$).

4 | DISCUSSION

Results from the comparison of *P. edwardsi* inhabiting disturbed and undisturbed forests in Ranomafana indicate that sifakas in disturbed forests are both ^{13}C- and ^{15}N-depleted relative to sifakas in undisturbed forests. Sifakas in disturbed and undisturbed forests in RNP have on average a 1‰ difference in $\delta^{13}C$ (Fig. 4, Table 2). While statistically significant, this difference is not considered biologically important given that globally C_3 plants range between −23‰ to −31.5‰, with an average of −28.5‰ (Kohn, 2010). In tropical rainforest mammals in the Amazon, differences in $\delta^{13}C$ composition of collagen span a range of 3‰ (van der Merwe & Medina, 1991), thus the range observed in the RNP sifakas is minimal.

Differences in $\delta^{15}N$ between sifakas in disturbed and undisturbed forests are, in contrast, biologically significant. $\delta^{15}N$ is highest at 4‰ for sifakas inhabiting undisturbed sites and lowest at 1.5‰ for sifakas inhabiting disturbed sites (Fig. 4, Table 2). As each trophic level is, on average, represented by a 3‰ difference in stable nitrogen (DeNiro & Epstein, 1981), a difference of 2.5‰ in populations of the same species of sifaka inhabiting forested areas within 10 km of each other and which are comparable except in degree of disturbance is noteworthy. The lousefly shows a smaller but distinct offset, with flies from *P. edwardsi* in Talatakely being on average ~1‰ $\delta^{15}N$-depleted relative to *P. edwardsi* in Vatoharanana (Fig. 4, Table 2).

Determining factors responsible for lower values of ^{15}N in sifakas at Talatakely is complex. Because isotopic composition varies depending on food items most commonly exploited, the challenge arises when an animal incorporates a variety of food items from different trophic levels (e.g., consumption of plants and insects) and even within a single trophic level. Although *P. edwardsi* is a folivore, direct comparisons between isotope composition and diet are difficult owing to the breadth of the *P. edwardsi* diet in RNP whose diet comprises over 45 genera of plants (Arrigo-Nelson, 2006).

The activities of *P. edwardsi* at RNP are closely monitored as part of several long-term research studies out of Centre ValBio and data from these studies are an invaluable complement to research presented here. The sifakas at Talatakely and Vatoharanana have comparable diets in terms of the plant taxa exploited: 97.4% and 87.4% of the plants consumed in Talatakely and Vatoharanana, respectively, come from the same 45 genera (Arrigo-Nelson, 2006). However, at the species level, *P. edwardsi* in Valohoaka has a more diverse diet (50% of their time is spent on 5 genera and 8 species) than does *P. edwardsi* at Talatakely (54.9% of their time is spent on 3 genera and 4 species).

A good question is whether legumes are consumed by *P. edwardsi*. Legumes, as nitrogen fixers, typically have values of $\delta^{15}N$ close to 0‰ (Ehleringer & Rundel, 1989). Animals that ingest legumes in any significant quantity will likewise be lower in ^{15}N. Leguminous plants are not very common at the 3 study sites, although they are more common in Talatakely: 3 genera of leguminous trees are found at Valohoaka and account for 1.70% of the plants surveyed by Arrigo-Nelson (2006), while 4 genera are found at Talatakely and have a relative abundance of 3.36%. In contrast, *P. edwardsi* consumes more leguminous plants (tree species and non-tree species) at Valohoaka (6.29% of total diet) than at Talatakely (4.18% of the total diet). Therefore, it is unlikely that legumes play a significant role in depletion of $\delta^{15}N$ in *P. edwardsi*, and if they did, one would expect to see sifakas at Valohoaka slightly more $\delta^{15}N$-depleted.

A more likely factor in the depletion of $\delta^{15}N$ is the consumption of *B. clavata* (Loranthaceae), a hemiparasitic mistletoe endemic to Madagascar. In RNP, sifakas inhabiting disturbed forests consumed *B. clavata* almost twice as frequently as sifakas in undisturbed forests (29% and 14% of the total diet, respectively (Arrigo-Nelson, 2006)). Similarly, Irwin (2008b) found that *P. diadema* in fragmented forests in Tsinjoarivo 300 km north of RNP consumed *B. clavata* as a staple food year round during both dry and wet seasons, spending between 30% to 40% of their feeding time on *B. clavata*, whereas *P. diadema* from continuous forests used *B. clavata* primarily as a fallback food during the dry season (devoting 28–30% of their feeding time to this resource). Nutritional analysis of *B. clavata* shows that tannins in mature leaves are lower in the disturbed site in RNP but otherwise nutritionally comparable between disturbed and undisturbed sites in RNP (Arrigo-Nelson, 2006). We found that *B. clavata* in Talatakely and Valohoaka is low in $\delta^{15}N$, particularly for a non-leguminous plant

(Table 2). $\delta^{15}N$ in *B. clavata* is lower at Talatakely than Valohoaka, although as noted above, not significantly so. What could account for lower nitrogen values at Talatakely is the fact that *P. edwardsi* is consuming twice as much *B. clavata* there.

The relationship between depletion of ^{15}N and nutritional status is complex. Fasting has been associated with ^{15}N enrichment in birds in some studies (e.g., Cherel, Hobson, Bailleul, & Groscolas, 2005; Hobson, Alisauskas, & Clark, 1993), presumably due to catabolism of protein stores and fractionation during the formation of nitrogenous wastes (Hobson et al., 1993). Other bird studies which examined less extreme food restriction found modest $\delta^{15}N$ enrichment (Williams, Buck, Sears, & Kitaysky, 2007) or no $\delta^{15}N$ enrichment (Kempster et al., 2007). Loudon et al. (2007) found nitrogen enrichment in ring-tailed lemurs (*Lemur catta*) in suboptimal health. Crowley et al. (2013) found slightly higher $\delta^{15}N$ (~0.5‰) in *Cheirogaleus crossleyi* in the fragmented forests of Tsinjoarivo, but were unable to ascertain if the increase in $\delta\ ^{15}N$ was due to increased insect consumption or nutritional stress. Ben-David, McColl, Boonstra, and Karels (1999), however, found no effect between food restriction and isotope composition, although it was noted that physiological effects (i.e., stable nitrogen composition) may have been obscured by diet selection. If this is the case for sifakas, the use of fallback foods is especially relevant. The consumption of *B. clavata* has other implications in addition to depletion of $\delta^{15}N$. Research suggests that fallback foods play an important role in primate population densities, either directly (e.g., availability of a fallback food as a limiting resource) or indirectly (e.g., causing social stress which in turn may influence access to a fallback food) (Irwin, 2008b). Use of fallback foods for which lemurs are not adapted has other deleterious effects. Sauther and Cuozzo (2009) found that ring tailed lemurs (*L. catta*) in Beza Mahafaly rely heavily on fruit from the tamarind tree (*Tamarindus indica*), resulting in severe tooth wear and tooth loss.

The long-term effects of habitat disturbance on primate populations remain a central conservation concern. Research has shown that selective logging has many effects, for example, physiological, ecological, behavioral, and here, a combination of biotic and biogeochemical. Studies that examine these effects individually often produce opposing conclusions. For example, Gerber et al. (2012) studied population densities of sifakas in RNP in disturbed versus undisturbed forests (i.e., a compositional biodiversity attribute) and found no difference in population density between disturbed and undisturbed forests. Pochron et al. (2004) examined demographic trends (i.e., a functional biodiversity attribute) in sifakas over 25+ years in a selectively logged forest in RNP. They found that certain life-history characteristics, notably high infant and adult mortalities, resulted in a low net reproductive growth rate which could, in turn, make sifakas vulnerable to local extinction. Focusing on the connections between and among different components and attributes of biodiversity affected by anthropogenic disturbance can provide greater insight and assist conservation management programs.

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