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Habituation of Greater Bamboo Lemurs (*Prolemur simus*) in the Vatovavy forest, Madagascar

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Abstract: Habituation is a preliminary process, allowing observers to become more familiar with animals and record their behavior. Few studies have described the habituation process for non-human primate species and there is a dearth of information on the habituation process among lemurs. This study describes the habituation of the Critically Endangered greater bamboo lemur (*Prolemur simus*). We used continuous focal animal sampling (384 hours) to collect behavioral data on seven individuals from two groups in the Vatovavy forest, southeastern Madagascar. We categorized our behavior data into two response types: habituated behaviors and non-habituated behaviors. Study animals were considered habituated when they showed an increased tolerance to human observers permitting focal animal data collection with minimal non-habituated responses. There were no significant differences among individuals for both habituated and non-habituated behaviors, therefore, all data were pooled together. Distance from observer and height of animals in the forest significantly decreased during the habituation process. By the end of the study, the frequency of habituated behaviors significantly increased. In conjunction with previously reported findings for this species, this study concludes that greater bamboo lemurs can be habituated in approximately 13–16 weeks.

Keywords: Habituation, Kianjavato, lemur, Strepsirrhini

Introduction

Habituation is a crucial tool for studying the behavior of wild animals in their natural habitat (Crofoot *et al*. 2010). Through this process, field investigators aim to increase the study animals' tolerance to their presence (Allan *et al*. 2020), thereby increasing the visibility of their subjects to enable the identification of individuals and their relationships, and allow consistent recording of behaviors (Goldsmith 2005; Williamson and Feistner 2011). Although most field-based primatological studies rely on habituation, species-specific information is often lacking (Fedigan 2010; Williamson and Feistner 2011).

Despite many studies having used habituation techniques to answer behavioral questions (Bertolani and Boesch 2007), only a few have described the habituation process for non-human primate species (Tutin and Fernandez 1991; Krunkelsven *et al*. 1999; Cipolletta 2003; Blom *et al*. 2004; Sommer *et al*. 2004; Bertolani and Boesch 2007; Doran-Sheehy *et al*. 2007; Ando *et al*. 2008), and fewer still for non-hominoids (Rasmussen 1998; Jack *et al*. 2008). Among lemur studies, there is a dearth of information on the habituation process, often only identifying the duration of habituation without describing the process or the behavioral changes (Sterling 1993; Tan 1999). Since habituation is an important first step for long-term field studies (Ando *et al*. 2008), detailed descriptions of habituation programs could be useful for lemurs, which are considered the most endangered group of mammals (Schwitzer *et al*. 2014).

Here we describe and evaluate the response of the Critically Endangered greater bamboo lemur (*Prolemur simus*) (Ravaloharimanitra *et al*. 2020) to habituation efforts conducted by repeated exposure to human observers. More specifically, we examine how some behaviors, distance to observer, and height in trees varied during the habituation process. An individual was considered habituated when we were able to collect focal animal data with minimal responses to observer presence (Hanson and Riley 2008). Based on the work of Tan (1999), we predict these animals would be sufficiently habituated to permit focal follows in approximately four months.

Methods

Ethics Statement

This study was conducted in agreement with the authorization of the Direction des Eaux et Forêt de Madagascar (research authorization: 141/18/MEEF/SG/DGF/DSAP/SCB. Re) and Omaha's Henry Doorly Zoo and Aquarium's Institutional Animal Care and Use Committee guidelines (97-001, 12-101). All procedures were carried out with permission of the Malagasy Government and complied with the Code of Best Practices for Field Primatology. The darting was carried out by an experienced Malagasy team overseen by an American board-certified veterinarian; details of the procedure are described in the Collaring section (below).

This study is part of a long-term monitoring program in the Kianjavato area of Madagascar. Radio collars are used to monitor lemur species in this region to facilitate data collection on such as behaviors, home ranges, reproduction, dispersal, and demographics. While habituation could be achieved without the use of radio collars, and while darting animals can have an immediate negative stimulus against habituation, we felt the long-term behavioral assessment of the ecology of the species is best achieved through the use of radio collars.

Study site

We conducted this study in Vatovavy forest (21.39819 S, 47.94281 E; Fig. 1) located in southeastern Madagascar, in the Vatovavy-Fitovinany Region. With an area of 640 ha and an altitude of 90–530 m (Holmes 2012), Vatovavy is wet, hot lowland to midland forest with varying levels of degradation (Emberton 1996). This forest is dominated by two vegetation types: humid forest and secondary lowland forest, which is the result of slash-and-burn agriculture (Manjaribe *et al*. 2013).

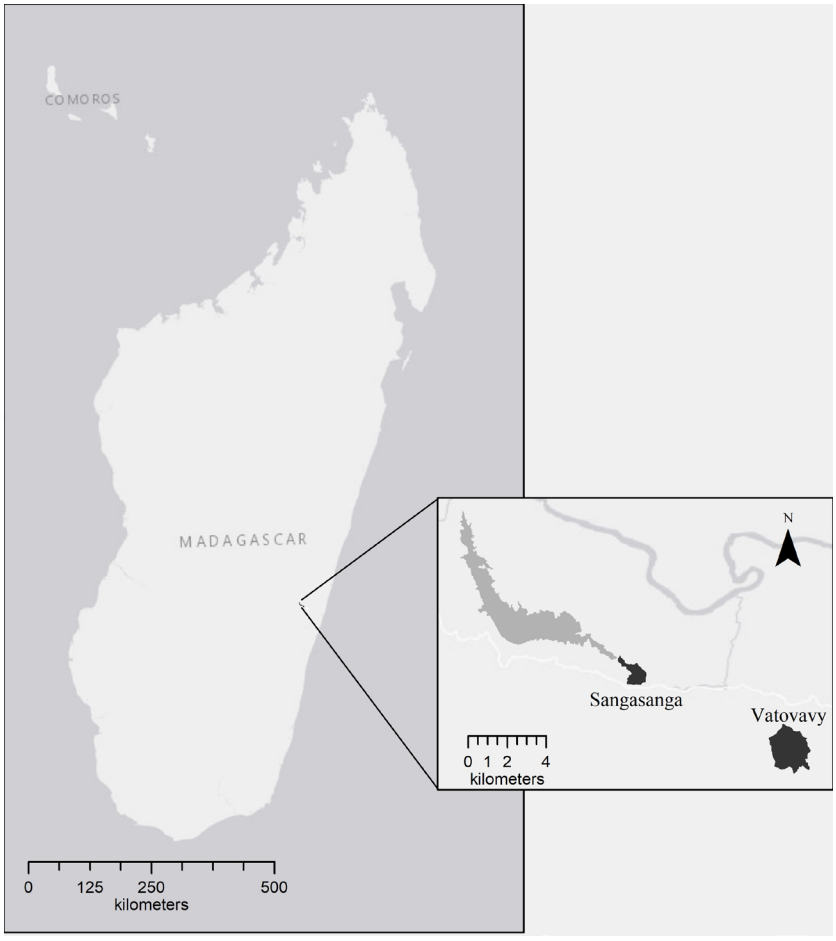

Figure 1. Location of the study site in Madagascar. Highlighted areas in the inset map represent forest fragments, with the darkest fragments being Vatovavy and Sangasanga.

Collaring

Individuals were sedated using 10 mg/kg Telazol (Zoetis) delivered by dart from a CO_2-powered injection rifle. Only adults as determined by weight and molar eruption were fitted with a radio collar (Advanced Telemetry Systems M1545; Fig. 2). The weight of the collar was around 25 g, which is below the 5% threshold of the subject's weight that ranged from 2.0 to 2.8 kg, corresponding to the Guidelines of the American Society of Mammalogists (Sikes and Animal Care and Use Committee of the American Society of Mammalogists 2016).

During the capture event, the adult males displayed an alert response upon our approach. Then, all group members moved to a nearby tree and remained there watching us as we came nearer. This provided opportunities to capture subject animals at close range. Once the subject animal was captured, the other adults in the group either reacted by fleeing or moved to the highest part of the canopy. All immobilized animals underwent a health assessment and then were held in cloth bags until they regained full mobility, at which point they were returned to the forest at the exact location of their capture. There were no injuries or deaths as a consequence of the captures.

Once sufficiently habituated to permit reliable data collection, radio collars on females were changed to nylon collars with aluminum pendants and no transmitter. Since males are the dispersing sex (Tan 2000; Frasier *et al*. 2015), we continued to equip them with radio collars to facilitate location of the study groups and the individual in the case of dispersal.

Behavioral data collection

We started habituating three greater bamboo lemurs, two males from the northeast group and one female from the northwest group, in November 2016. In February 2017, we added another four individuals from these groups, one male and one female from the northeast group, and one male and one female from the northwest group. Data were collected over 18 weeks between November 2016 and April 2017. It should be noted that these two groups comprised more than just the seven collared individuals and that other members of the group were also habituated during this process. However, due to the monomorphic nature of the species, data were only collected on the radio-collared individuals.

Figure 2. A greater bamboo lemur with a radio collar. Photograph by Ando Rakotonanahary.

Table 1. Definitions of behaviors observed during the habituation process of the greater bamboo lemurs in Vatovavy forest.

Behavior category	Description
Non-habituated	
Avoid	Having detected the presence of the observer, the animal(s) move(s) away rapidly emitting alarm vocalization
Curious	Animal(s) watching the observer, or moving to a position to obtain a better view of the observer
Habituated	
Feed	Animal(s) continue(s) feeding normally even after noticing the presence of the observer
Rest	Animal(s) show(s) no reaction to the presence of the observer, including sitting or lying down; not involved in any other activity
Move	Focus animal(s) walk, run, climb, or jump
Social behavior	Includes grooming, playing, aggressive, or sexual behavior

Following Williamson and Feistner's (2011) methods, after locating animals using radio telemetry, we tried to keep a distance from the lemurs greater than that which provokes flight, approaching focal animals slowly, talking softly, and avoiding sudden gestures. As primates are sensitive to the number of people present, it is better to work with the same small group of people (Williamson and Feistner 2011). We used, therefore, the same three observers simultaneously during the entire habituation process.

During habituation, we used focal animal sampling with continuous recording methods (Altmann 1974; Martin and Bateson 1993). We conducted six-hour follows, Monday through Friday, and switched the focal individual between groups each day. All individuals were exposed to observers at least two days per week. Behavioral data collection started immediately upon locating the animals and included all behavioral responses to observer presence (Table 1). We used a GPS unit (Garmin GPSMAP 64S) to record the location of the individuals every fifteen minutes. We used a range finder (Nikon Forestry Pro) to record observer-primate distance, and we estimated the height of the focal animal from the ground. We categorized our behavior data into two response types: habituated behaviors (feeding, resting, moving, and social behavior) and non-habituated behaviors (avoidance and curiosity). We collected 384 hours of behavioral data with an average of 54 hours (range = 30–95 hours, standard deviation = 26 hours) per individual. For information on individuals, groups, and the total hours of data per individual see Table 2.

Table 2. Information on the greater bamboo lemur individuals followed during the habituation period in Vatovavy forest. M = male, F = female, NE = Northeast Group, and NW = Northwest Group.

ID	Name	Sex	Group	Date of first observation	Date of last observation	Days of observation
VAVY16.4	Drogon	M	NE	10/04/2016	09/13/2018	13
VAVY16.5	Tyrion	M	NE	10/05/2016	11/15/2018	16
VAVY16.6	Daenerys	F	NW	11/24/2016	11/15/2018	12
VAVY17.1	Bran	M	NW	02/06/2017	06/06/2018	6
VAVY17.2	Snow	M	NE	02/08/2017	11/15/2018	5
VAVY17.3	Nymeria	F	NE	02/08/2017	11/15/2018	6
VAVY17.4	Arya	F	NW	02/08/2017	11/15/2018	6

Statistical analysis

All analyses were run using R (v3.6.1; R Core Team 2019). All tests were set at the same significance level ($\alpha = 0.05$). A Shapiro-Wilk test determined that our data were not normally distributed (distance: $W = 0.845$, $p < 0.001$; height: $W = 0.864$, $p < 0.001$) and we therefore used non-parametric tests.

We used Fisher's exact test to compare average monthly frequency of habituated and non-habituated behaviors between November 2016 and January 2017 for the following animals: VAVY16.4 (male), VAVY16.5 (male), and VAVY16.6 (female). We also used Fisher's exact test to compare average monthly frequencies of habituated and non-habituated behaviors for all individuals between February and April 2017. In addition, the use of Fisher's exact test confirmed that we can combine and analyze all individuals as one data set.

Due to our small sample size, we factored our data into bi-weekly sets (i.e., set one: week one and two, set two: week three and four, etc.) to create a stronger statistical analysis. We ran Kruskal-Wallis tests to compare the frequency of habituated behaviors, non-habituated behaviors, heights and distances between these sets. Then, we ran *post hoc* tests with a Tukey method.

Results

Comparison between individuals

The Fisher's exact test found no significant differences ($Fr = 2.667$, $df = 2$, $p = 0.263$) among individuals VAVY16.4, VAVY16.5, and VAVY16.6 between average monthly frequencies of behaviors from November 2016 and January 2017. Similarly, there were no significant differences ($Fr = 4.087$, $df = 6$, $p = 0.665$) among all individuals in average monthly frequencies of behaviors between February and April 2017. As a result, we pooled the data from all individuals by month in our analysis of the habituation process.

Response type

We found that the frequency of habituated and non-habituated behaviors changed over the course of the habituation process. The Kruskal-Wallis test revealed a significant decrease in non-habituated ($H = 38.426$, $df = 8$, $p < 0.001$) and increase in habituated behaviors ($H = 38.05$, $df = 8$, $p < 0.001$) over the study period. *Post hoc* comparison confirmed that both non-habituated and habituated behaviors during the first two sets (weeks 1–4) were significantly different ($p < 0.05$) than the respective behaviors from the last three sets (weeks 13–18; Tables 3 and 4).

Distance

Statistical analysis showed a significant decrease in distance between the observers and the greater bamboo lemurs ($H = 1563.5$, $df = 8$, $p < 0.001$) over the course of the study based on a Kruskal-Wallis test. The *post hoc* test revealed no significant differences in distances to the observer between sets one and two, sets three and six, sets four and five, and sets seven, eight, and nine (Table 5). All other bi-weekly comparisons were significantly different ($p < 0.001$). We found that the horizontal distance between the observer and the greater bamboo lemurs decreased over the course of the habituation process, with individuals performing most of their normal activity (i.e., non-habituated behaviors) at a distance between 6 and 10 m by the end of the study (Fig. 3a).

Height

Similar to distance between observer and focal animal, a Kruskal-Wallis test showed a significant decrease in height of the greater bamboo lemurs in the canopy over the course of the study ($H = 1622.4$, $df = 8$, $p < 0.001$). The *post hoc* test found most bi-weekly sets were significantly different from each other ($p < 0.001$) except for set five (weeks 9–10), which was not significantly different from sets six, seven, or nine (Table 6). During the first four sets of the study, the focal animals were over 10 m high; by the fifth set

Table 3. *Post hoc* test results for bi-weekly (sets) comparisons of frequency of habituated behaviors for greater bamboo lemurs. Bold text indicates significant differences between sets.

	Set 1	**Set 2**	**Set 3**	**Set 4**	**Set 5**	**Set 6**	**Set 7**	**Set 8**
Set 2	1.000							
Set 3	0.998	0.9998						
Set 4	1.000	1.000	1.000					
Set 5	0.988	0.998	1.000	1.000				
Set 6	0.9522	0.9821	1.000	0.9989	1.000			
Set 7	**0.0089**	**0.0114**	0.2445	0.2488	0.0951	0.4160		
Set 8	**0.0111**	**0.0142**	0.2722	0.2725	0.1122	0.4539	1.000	
Set 9	**0.0089**	**0.0114**	0.2445	0.2448	0.0951	0.4160	1.000	1.000

Table 4. *Post hoc* test results for bi-weekly (sets) comparisons of frequency of non-habituated behaviors for greater bamboo lemurs. Bold text indicates significant differences between sets.

	Set 1	**Set 2**	**Set 3**	**Set 4**	**Set 5**	**Set 6**	**Set 7**	**Set 8**
Set 2	1.000							
Set 3	0.9973	0.9996						
Set 4	1.000	1.000	1.000					
Set 5	0.9968	0.9997	1.000	1.000				
Set 6	0.9536	0.9815	1.000	0.9987	0.9998			
Set 7	**0.0121**	**0.0149**	0.3048	0.2694	0.0705	0.4659		
Set 8	**0.0146**	**0.0181**	0.3323	0.2911	0.0924	0.5000	1.000	
Set 9	**0.0065**	**0.0078**	0.2242	0.2054	**0.0471**	0.3594	1.000	1.000

Table 5. *Post hoc* test results for bi-weekly (sets) comparisons of frequency of distance from observer for greater bamboo lemurs. Bold text indicates significant differences between sets.

	Set 1	**Set 2**	**Set 3**	**Set 4**	**Set 5**	**Set 6**	**Set 7**	**Set 8**
Set 2	0.98534							
Set 3	**<0.001**	**<0.001**						
Set 4	**<0.001**	**<0.001**	**<0.001**					
Set 5	**<0.001**	**<0.001**	**<0.001**	0.48603				
Set 6	**<0.001**	**<0.001**	0.32266	**<0.001**	**<0.001**			
Set 7	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**		
Set 8	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	0.9997	
Set 9	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	0.9997	1.000

Table 6. *Post hoc* test results for bi-weekly (sets) comparisons of frequency of height of animals for greater bamboo lemurs. Bold text indicates significant differences between sets.

	Set 1	**Set 2**	**Set 3**	**Set 4**	**Set 5**	**Set 6**	**Set 7**	**Set 8**
Set 2	**<0.001**							
Set 3	**<0.001**	**<0.001**						
Set 4	**<0.001**	**0.0005**	1.000					
Set 5	**<0.001**	**<0.001**	**<0.001**	**<0.001**				
Set 6	**<0.001**	**<0.001**	**<0.001**	**<0.001**	0.18816			
Set 7	**<0.001**	**<0.001**	**<0.001**	**<0.001**	0.99977	0.60467		
Set 8	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**0.03590**	**<0.001**	**0.01492**	
Set 9	**<0.001**	**<0.001**	**<0.001**	**<0.001**	0.32480	**<0.001**	0.16087	0.99652

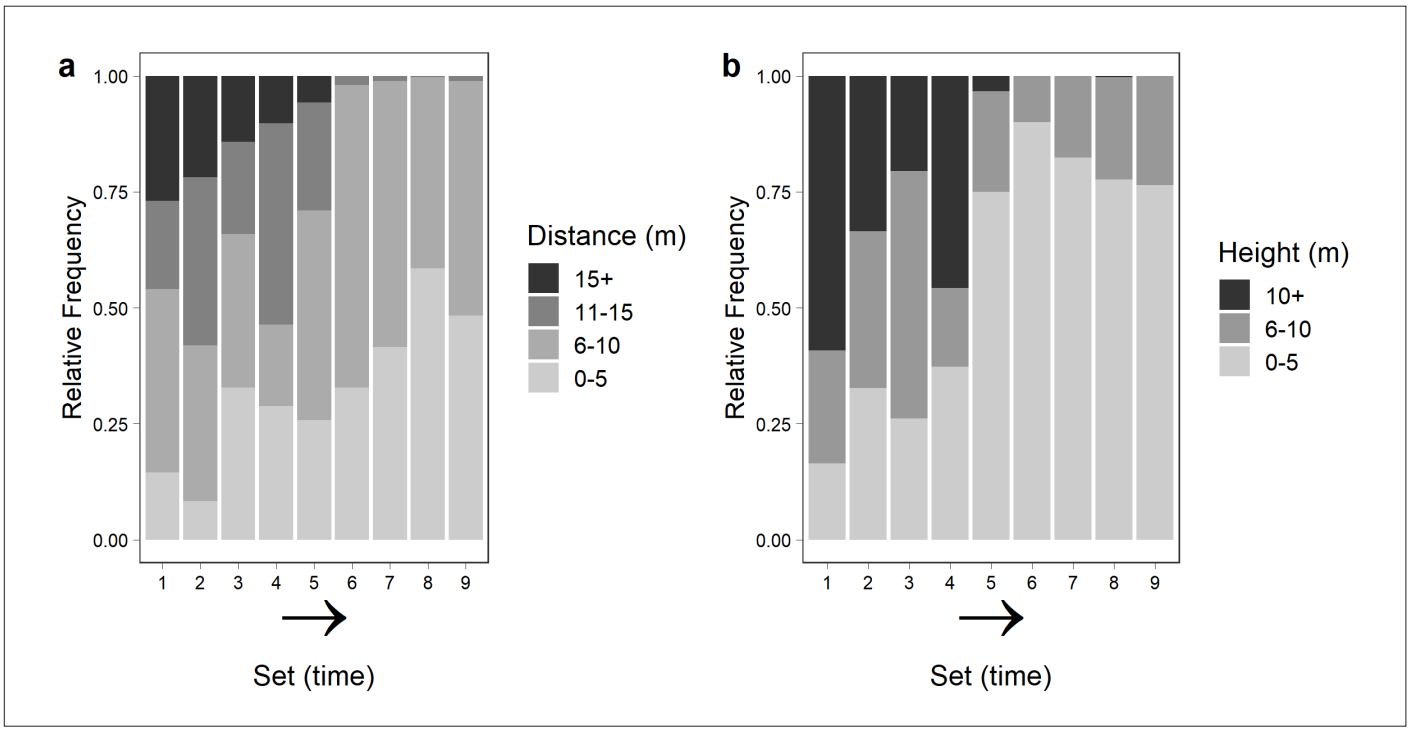

Figure 3. Reduction of lemur-observer distance (a) and lemur height in trees (b) from November 2016 to April 2017 in Vatovavy, Madagascar. Each time-interval ('set') corresponds to consecutive two-week observation periods.

(weeks 10–11) of the process, all individuals decreased their height in the forest to between six and ten meters. Indeed, the greater bamboo lemurs became so tolerant of our presence that by the end of the study they occasionally fed on the ground (Fig. 3b). There was no significant difference between sets three and four, possibly due to the break in the study. Curiously, set eight was significantly different from sets five, six, and seven, though the following bi-weekly set (i.e., nine) was not significantly different from these periods.

Discussion

Habituating animals requires consistent contact between the same groups of animals and observers (Ando *et al*. 2008). This reflects what happened with our greater bamboo lemur population at Vatovavy, which initially showed a propensity for avoidance and curiosity behaviors. By 13–16 weeks, these lemurs showed regular signs of habituation and by 18 weeks consistently displayed high frequencies of habituated behaviors. Habituation of other bamboo lemur species (*Hapalemur*) in Ranomafana National Park was accomplished in one month, while greater bamboo lemurs were more cautious in the presence of humans, with habituation taking four months (Tan 1999). In agreement with the findings of Tan (1999), habituation of greater bamboo lemurs also took approximately four months at Vatovavy. The gap in our observation period did not appear to severely hamper the habituation process of our study population.

As was anticipated based on previous primate studies (Johns 1996; Blom *et al*. 2004; Hanson 2017), during the habituation process greater bamboo lemurs increased the frequency of habituated behaviors and decreased the frequency of non-habituated behaviors. While the significant changes in frequency of habituated and non-habituated behaviors occurred by set seven (weeks 13–14; Tables 3 and 4), it is possible that the study animals started altering their behavior as early as the third set (weeks 5–6). The lack of significant differences in behaviors between set three and sets seven, eight, and nine, suggest that the frequency of behaviors had changed enough after the first six weeks to not be significantly different by the time habituation was fully achieved. This is not to say that greater bamboo lemurs were completely habituated after six weeks, only that the study population was becoming habituated to our presence by this time.

The distance of the study animals to the observer and height in the forest further support our suggestion that their behavior started to change as early as set three (weeks 5–6) or two (weeks 3–4), respectively (Fig. 3a and Fig. 3b). It is possible that the greater bamboo lemurs recognized that we did not represent a threat as far as our ability to ascend vertically, and thus started reducing the height in the forest earlier. However, they were still wary of our presence, thus maintaining a greater horizontal distance between us for a longer duration. This would also explain why by set five (weeks 9–10) there were fewer differences in height, while horizontal distance continued to change until set seven (weeks 13–14).

Habituation can have a negative influence on primate populations. For example, habituated primates are an easier

target for poachers and hunters (Goldsmith 2005; Williamson and Feistner 2011). Habituation also creates the risk of infectious disease transmission from observers to non-human primates (Woodford *et al*. 2002; Wolfe 2005; Williamson and Feistner 2011) and induces the stress response in the target animals (Jack *et al*. 2008). However, reliable location and identification of individuals is necessary to understand many aspects of wildlife behavior and frequently requires habituation and the use of markers, such as collars.

While habituation can be achieved with less invasive techniques, we felt the use of radio collars was important to the success of this program. For example, individuals in some species of primates can be distinguished easily via sexual dimorphism, other species have no readily noticeable differences among individuals (Juarez *et al*. 2011). Greater bamboo lemurs are a sexually monomorphic primate, and the use of radio collars allowed us to identify individuals, habituate them, and facilitate the efficient location of focal individuals and groups. In addition, the use of collars did not appear to impact the reproductive abilities or survival of greater bamboo lemurs, as Frasier *et al.* (2015) reported high fecundity rates and low adult mortality of individuals that were collared for years. We therefore felt confident that the long-term benefits of using radio collars outweighed the short-term complications of habituation that might be experienced. It is important to note that habituation of non-human primates may take longer if they have been hunted or have had negative interactions with humans (Williamson and Feistner 2011).

Habituation has played an important role in facilitating conservation efforts for greater bamboo lemurs, attracting researchers and ecotourists, thus deterring hunting and poaching. Indeed, where appropriate, the continued practice of habituation should be more readily reported to help guide future research of primates in general, and especially of the numerous threatened lemur species (Schwitzer *et al*. 2014).

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