



Costs and Benefits of Radio-collaring on the Behavior, Demography, and Conservation of Owl Monkeys (*Aotus azarai*) in Formosa, Argentina

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Abstract The benefits to researchers of capturing and collaring free-ranging primates are numerous, but so are the actual and potential costs to the individuals. We aimed to 1) evaluate quantitatively the possible demographic long-term costs of radio-collaring a free-ranging primate species, and 2) evaluate qualitatively the costs to the subjects and the overall benefits to the research program that results from monitoring a large number of groups with collared individuals during many years. Between 2000 and 2009, we captured, recaptured, and radio-collared 146 owl monkeys (*Aotus azarai*) to study the behavior, demography, and genetics of the species. To evaluate the potential long-term costs of the collaring procedures on the population, we compared the demographic composition of groups ($n=20$) in our core study area with those of undisturbed groups ($n=20$) in a control area within the same forest. Groups in both areas ranged in size between 2 and 5 individuals. Surprisingly, group size tended to be larger among the study groups owing to more infants and juveniles in those groups than in the control groups. The benefits to the research program have included, among others, the reliable identification of individuals, increased sample sizes, the recovery of specimens, studies of dispersal, outreach activities, and conservation education. Still, some of the benefits will become tangible only when the project persists on time; is fully approved and supported by local authorities; and has broad community participation, as well as

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conservation and education goals. Thus, any serious initiative to capture and collar individuals should be the result of an extremely careful evaluation of benefits and costs.

Keywords Darting · Demography · Dimorphism · Dispersal · Radio-collar · Telemetry

Introduction

Attempts to capture and collar primates in the 1980s and 1990s (Bearder and Martin 1980; Brett *et al.* 1982; Campbell and Sussman 1994; Charles-Dominique 1977; de Ruiter 1992; Dietz *et al.* 1994; Fedigan *et al.* 1988; Glander *et al.* 1991; Gursky 1998; Jones and Bush 1988; Karesh *et al.* 1998; Müller and Schildger 1994; Savage *et al.* 1993) have been followed by an increase in the use of these procedures during the last decade (Honest and Macdonald 2003; Müller 1999), including the incorporation of new technologies like satellite tracking and biotelemetry (Markham and Altmann 2008). In most instances, the primary reason for radio-collaring primates has been the need to locate and follow elusive individuals; but there are many other reasons that have not been thoroughly considered. Although individuals can be reliably distinguished in most primate species via natural marks and scars, in other species there are no readily noticeable differences among individuals. For example, in some sexually monomorphic primates, the sexes cannot be easily differentiated based on body size differences or appearance of the external genitalia (Fernandez-Duque and Rotundo 2003). In these taxa, radio-telemetry makes it possible to locate elusive individuals and also provides permanent identification of individuals for long-term behavioral and demographic studies.

Capturing and collaring free-ranging primates is a complex process that carries actual and potential costs to the individual, the population, the researchers, and the research program (Ancorenaz *et al.* 2003; Jolly *et al.* 2003). Unfortunately, little information is available on these costs and how to mitigate them. The most obvious and understood potential negative effects are those related to the well-being of the captured individual. Subjects may be severely wounded or die during the procedures (Brett *et al.* 1982; Karesh *et al.* 1998). In turn, the death of a captured individual could have devastating consequences for the research program if the circumstances surrounding the event are unclear to local authorities. There are also potential costs to the subjects once they are released. For example, the collaring of individuals may result in injured and infected necks when the collars are ill fitting (Müller and Schildger 1994), and the wearing of a collar or a mark could influence the behavior of the captured individual or its conspecifics (Teichroeb *et al.* 2005). There may also be costs associated with the reintegration of the captured individual into its social group. For example, low-ranking long-tailed macaque males (*Macaca fascicularis*) were sometimes threatened by conspecifics after being removed from the group for 2 d (de Ruiter 1992). Finally, there may be other potential long-term costs that are more difficult to identify and quantify. For example, if the collar results in a loss or gain of weight by the subjects, these changes in body mass could later influence reproductive function.

The Owl Monkey Project to study *Aotus azarai* in the Argentinean Chaco began in 1996. A few years after the project began, it became clear that most of our research questions could not be effectively addressed without the unequivocal

identification of individuals (Fernandez-Duque and Huntington 2002). Such identification was not possible in this sexually monomorphic taxon without the capturing and marking of individuals. Thus, in 2000 we began to capture and collar individuals regularly in the focal population (Fernandez-Duque and Rotundo 2003).

After having captured 146 individuals, we present the results of a study that had 2 main objectives: 1) to conduct a quantitative evaluation of the possible long-term reproductive costs of collaring individuals as assessed from the comparison of the demographic composition of collared vs. noncollared groups and 2) to conduct a qualitative evaluation of the collaring costs to the subjects and the overall collaring benefits to the researcher. Regarding a quantitative evaluation of the possible long-term costs of radio-collaring, our primary motivation was to evaluate if the procedures had negative effects on the reproductive success of individuals that would subsequently be reflected in basic demographic parameters, e.g., group size. To accomplish this, we compared the demographic composition of groups ($n=20$) in our core study area with those of undisturbed groups ($n=20$) in a control area within the same forest. The main reason for doing a qualitative evaluation was to inform future primate studies that are considering the collaring of individuals and to improve our own procedures in the future.

Methods

Areas of Study

The study areas are located in the Guaycolec Ranch, 25 km away from the city of Formosa in the Argentinean Gran Chaco ($58^{\circ}11'W$, $25^{\circ}58'S$). The region consists of a matrix of grasslands dotted with patches of forests and transected by gallery forests that grow along rivers. Owl monkeys inhabit the gallery forests that grow along the Pilagá and Guaycolec rivers, as well as the patches of forests immersed in the grasslands.

The Owl Monkey Project has taken place primarily in a core area (*ca.* 300 ha) of gallery forest along the Pilagá River (Fig. 1). We have also occasionally worked in the gallery forests extending upstream and downstream from the core area, as well as in some of the isolated patches of forests (Fernandez-Duque 2009). For this study, we identified a control area of gallery forest 10 km upstream from the core area to evaluate the demographic characteristics of 20 undisturbed social groups. The core and control areas have similar forest composition and structure (Placci 1995).

Focal Groups

The social groups within the core area have been studied since 1997 (Fernandez-Duque *et al.* 2001, 2002; Wolovich *et al.* 2008). Between December 2000 and November 2009 we conducted 214 captures of 146 individuals to fit them with a radio ($n=121$), bead ($n=54$), or accelerometer collar ($n=22$). The total weight of the attachment system, i.e., transmitter, antenna, collar, and casing, ranged between 25 and 35 g for body masses between 1.0 and 1.5 kg. On 17 captures we did not fit the individual with a collar because it was too young and small ($n=3$), or because it was captured outside the study area, and we could not guarantee we would be able to

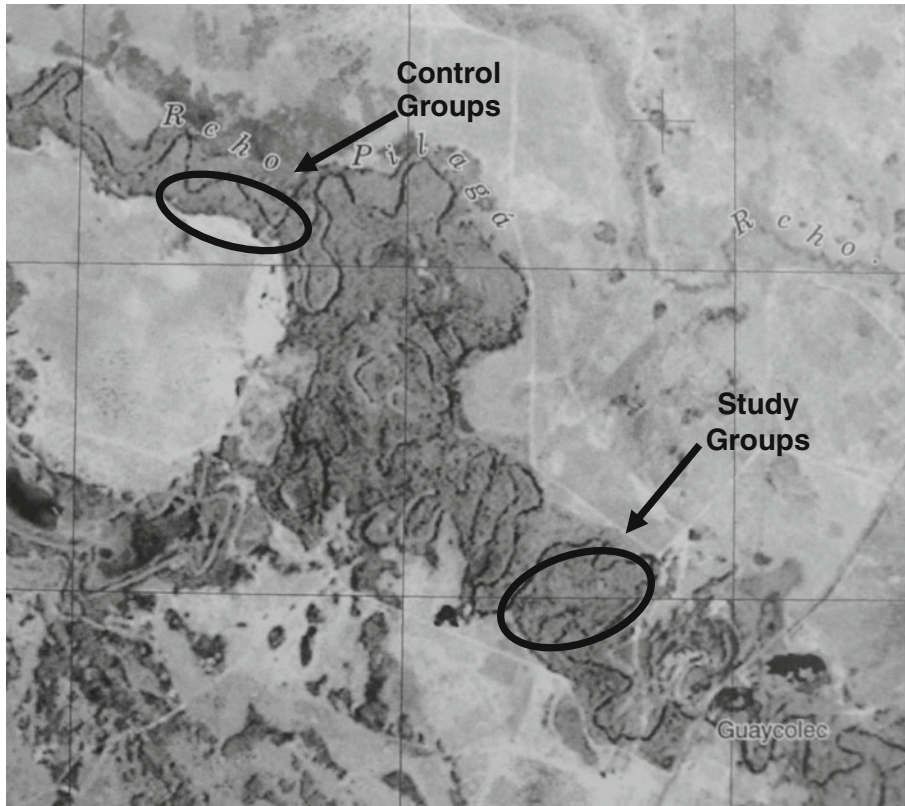


Fig. 1 Gallery forests along the Pilagá and Guaycolec rivers where we conducted the study. The core area is ca. 10 km downstream from the control area. The 2 areas of study are indicated with circles.

recapture it to remove the collar ($n=14$). We use various criteria to decide whether to fit the individual a radio, bead, or accelerometer collar. In each group, we fitted an accelerometer collar to 1 adult for a study of activity patterns between 2003 and 2006. Accelerometer collars (Actiwatch AW4) automatically record activity and store the data until downloaded to a computer (Fernandez-Duque and Erkert 2004, 2006; Fernandez-Duque and Rotundo 2003). These collars do not provide a radio signal and therefore it was necessary to fit a radio-collar to the other adult in the group. We normally fit radio-collars to juvenile individuals who are likely to disperse and to 1 philopatric adult, so that the group can be easily located. Finally, we sometimes provide bead collars to individuals that are between 1 and 2 yr old, unlikely to disperse and too small for the weight of a radio-collar. The procedures for capturing and marking individuals have been discussed elsewhere (Fernandez-Duque and Rotundo 2003) and are available at <http://www.sas.upenn.edu/~eduardof/Owlmonkeyproject.html>.

Demographic Data Collection

During the birth seasons of 2006–2007 and 2007–2008 (October–January, Fernandez-Duque *et al.* 2002), we collected information on group size, estimated

age of individuals, and infant presence from habituated groups in the core area ($n=20$) and from nonhabituated groups in the control area ($n=20$). We located groups in the core area using radio-telemetry or walking through their territories (Fernandez-Duque 2007a, b). To locate groups in the control area, we walked through the forest at dawn and at dusk when owl monkeys were consistently active. Most of the time we first detected the monkeys through the noises they made while moving, but then we took advantage of ambient light at dawn and dusk to count individuals and assess relative body size. When we were unsuccessful locating them, we sometimes played hoot calls (Moynihan 1964; Wright 1981, 1989), a low-pitch, relatively loud vocalization that is extremely effective in attracting individuals (Depeine *et al.* 2008). We stayed with each group for as long as they remained active in the morning—usually a few hours—or until it was dark at dusk. While following them, we recorded their positions with a GPS. The strict territoriality of owl monkeys and the relatively small overlap that exists among territories makes it possible to recognize different groups via a combination of spatial data and group composition data (Fernandez-Duque 2007a, b; Fernandez-Duque *et al.* 2008a, b; Wright 1978).

It is extremely difficult to sex owl monkeys in the field, as there is no obvious sexual dimorphism in body size or fur patterns, and the testes are relatively small (Dixson *et al.* 1980). We sexed all adults in the core area groups when captured, and precise group composition data for the core area groups was available via weekly monitoring of all groups. We were able to sex some individuals in the control area when the female was lactating and the nipples were prominent or if we were close enough to observe the testes. Otherwise, we assumed that there was 1 adult male and 1 adult female in each group.

To classify individuals in age categories we used a combination of demographic, behavioral, and morphometric data. We estimated age based on: 1) width and length of the dark stain produced by the subcaudal gland secretion, 2) relative body size, 3) presence of prominent nipples, 4) behavioral patterns, and 5) date of birth for individuals in the core area. Most individuals in the core area could be assigned precisely to an age category because they had been captured or because we had followed them since birth and could still recognize them by size (Fernandez-Duque 2009). We classified individuals as infants (0–11 mo), juveniles (12–23 mo), nonreproducing adults (>23 mo and still in natal group), or reproducing adults (>23 mo and not in natal group). We are usually able to estimate a relatively narrow age range for infants and juveniles because all births in the population occur between October and January (Fernandez-Duque *et al.* 2002), and owl monkeys are unequivocally of smaller size until they are 18 mo old. The classification of individuals as nonreproducing or reproducing adults is more difficult. Individuals do not reach full body mass or exhibit a fully developed subcaudal gland until they are *ca.* 4 yr of age (Fernandez-Duque 2004; Juárez *et al.* 2003).

In the control area, where we did not know the identity of the individuals, we used the aforementioned criteria to classify individuals into 3 age categories: adults, juveniles, or infants. Adults were the largest individuals in the group, and also had visually conspicuous subcaudal secretions on the ventral side of their tail (Dixson *et al.* 1980; Macdonald *et al.* 2008). We also classified an individual as adult if we observed it nursing or transporting an infant because infant carrying by nonadults is extremely infrequent (Fernandez-Duque *et al.* 2008a, b). We classified individuals as

juveniles if they were smaller than the adults in the group and showed some staining of the ventral side of their tail due to perianal secretions. Finally, we classified individuals as infants when they were the smallest individuals in the group, had no stains on the tail, and were carried by an adult when moving between trees. To compare the age structure in both areas we limited our analyses to 3 categories: infants, juveniles, and adults.

We compared group sizes in the control and core area via Mann-Whitney test for 2 independent samples.

Results

Potential Long-Term Effects: A Demographic Comparison

In the control area, we made contact with owl monkey social groups on 44 occasions during the study. On average, we spent *ca.* 1 h with each encountered group (mean: 58 min, range: 3–238 min). By using information on group composition and its location in the forest, we were able to differentiate 20 social groups. We also encountered 12 individuals that were ranging solitarily.

In both areas, groups ranged in size between 2 and 5 individuals (Table I). There was a larger proportion of groups with 4 and 5 individuals in the study area than there was in the control area. This difference was reflected in a somewhat larger average group size for the study than the control groups. The differences in average group size were statistically significant or showed a statistical trend (Table I, 2006–2007: $U=78$, $Z=-1.95$, $p=0.051$; 2007–2008: $U=112$, $Z=-2.23$, $p=0.026$).

In contrast, the age structure did not differ markedly between focal and control groups or between sampling points (Table II). As expected for a socially monogamous species, there were 2 adults in all groups. It was among juveniles and infants that we found some interesting differences in both sampling periods. In both years, there were fewer infants and juveniles in the control than in the focal population (Table II).

Costs to the Subjects

In a few instances, the fitting of radio-collars had apparently direct negative effects on the subject because of its weight and of its tightness. When retrieving exhausted collars, 4 individuals (3%) had scars on the dorsal side of the neck that we attributed to lacerations produced by the collar. In addition, our first captured individual died when a small twig got stuck between the collar and the neck while it was dispersing from the natal group ($n=1$).

On a few occasions, the removal of the captured individual from its social group during the capturing and restraining triggered social responses from conspecifics that had undesirable effects. Four captured individual were not accepted back into the group because their positions had already been taken by another same-sex individual ($n=3$; 4% of all individuals captured as resident adults) or it was rejected by its parents ($n=1$; 2% of all individuals captured while still in their natal groups). These individuals wandered as floaters for a relatively short time until they were found

Table I Size of groups observed in the control and the study areas in 2006–2007 and 2007–2008

Control group name	2006–2007		2007–2008		Study group name
	Control	Study	Control	Study	
Vargas01	3 (1)	3 (1)	4 (4)	3 (1)	A500
Vargas02	2 (1)	4 (1)	2 (1)	4 (1)	B68
Vargas03	3 (1)	2 (3)	–	2 (14)	C0
Vargas04	3 (2)	4 (3)	–	5 (3)	CC
Vargas05	2 (1)	4 (1)	–	5 (17)	Colman
Vargas06	3 (1)	3 (2)	–	3 (5)	D100
Vargas07	2 (1)	–	2 (1)	4 (2)	D1200
Vargas08	4 (1)	–	4 (1)	5 (2)	D1400
Vargas10	4 (2)	4 (3)	4(1)	4 (3)	D500
Vargas09	2 (1)	3 (1)	2(2)	2 (3)	D800
Vargas11	4 (2)	4 (4)	–	4 (14)	E350
Vargas12	3 (1)	5 (2)	–	4 (10)	E500
Vargas13	2 (1)	–	3 (2)	4 (1)	F700
Vargas14	2 (1)	5 (2)	3 (2)	5 (9)	F1200
Vargas15	2 (1)	5 (1)	3(2)	–	F1400
Vargas16	5 (1)	3 (1)	4 (2)	–	G1300
Vargas17	–	2 (1)	2 (1)	–	L100
Bajada Carpincho	–	2 (2)	2 (4)	–	P300
Vargas18	–	5 (2)	3(1)	4(1)	Parrilla
Vargas19	–	–	2(1)	3 (1)	Soldado
Mean group size	2.9	3.6	3.0	3.8	
Min size	2	2	2	2	
Max size	5	5	4	5	

In parentheses: Total number of times the group was contacted

dead or disappeared from the area of study. We subsequently decided to perform the procedures in the forest to minimize the time the individual is removed, and since then there have been no further problems of this kind.

There have been no significant changes in behavior that we could attribute to the collars. Radio-collared individuals have dispersed from their natal groups ($n=19$,

Table II Percentage of individuals in each age category in the control and focal groups during the 2 sampling periods

	Infants		Juveniles		Adults	
	Control	Study	Control	Study	Control	Study
2006–2007	4% (2)	12% (7)	26% (12)	33% (19)	70% (32)	55% (32)
2007–2008	13% (5)	15% (9)	18% (7)	32% (19)	70% (28)	53% (32)

In parentheses: total number of individuals observed

Fernandez-Duque 2009), mated, reproduced, and nursed ($n=27$ males, $n=22$ females).

Benefits to the Research Program

Unequivocal identification of individuals We were never able to recognize individual owl monkeys via natural marks. It was sometimes possible to recognize an individual based on its general appearance or gestalt, but never to an extent that we could recognize it outside its social group. However, radio-collars fitted for other reasons offered a conspicuous, reliable, and durable way of unequivocally identifying a large number of individuals ($n=146$) even after they dispersed from their social groups.

Habituation of groups The use of radio-collars allowed us to habituate as many as 15 groups by increasing the amount of time that researchers could remain in the proximity of groups during the habituation process. It also made it possible to contact as many as 10 groups regularly and in short succession, effectively shortening the period of habituation.

Increased sample sizes for demographic data We could monitor regularly (e.g. weekly, even daily) the composition of *ca.* 20 social groups. Field workers with vast experience in the use of radio telemetry can check the composition of ≤ 10 groups in 3–4 h. Since we began radio-collaring individuals, we have contacted an average of 3 groups per day during 2001–2008 (>7000 contacts with groups).

Dispersal and ranging patterns The use of radio-collars made it possible to follow 19 individuals from birth through dispersal and to obtain conclusive information on the final destination of 11 of them (Fernandez-Duque 2009). Radio-collars also allowed us to evaluate the simultaneous ranging of neighboring groups ($n=4$) and floaters ($n=2$) with the assistance of a relatively small number of field workers (Gustison *et al.* 2009).

Recovery of specimens The fast decomposition of corpses in the forest, combined with the presence of scavengers, makes the recovery of dead individuals a very rare event. During $>20,000$ h of work in the forest since 1997, we found the skeletal remains of only 4 noncollared owl monkeys. Conversely, during 2001–2009, we recovered the remains of 19 radio-collared individuals. The mortality signal programmed in the transmitter facilitates the finding of the individual relatively soon after its death. In most cases ($n=12$) we recovered only skeletal remains, but on 7 occasions we found the individual only a few hours after it had died, and most of the soft tissues were preserved. In one unusual and extreme circumstance, we recovered the body of a solitary adult female that had just died after an aggressive interaction with a female resident.

Conservation education and ecotourism The use of telemetry permitted us to bring primary-school and kindergarten students ($n=104$) from the city of Formosa to a wildlife reserve where we could readily find a social group following a radio-collared

individual. At dawn, 40 10-yr-old students who had never been in the forest took turns to observe wild owl monkeys for the first time in their lives. In addition, we organized 5 1-day community workshops that offered the opportunity to 100 adults from the city of Formosa and nearby areas to learn about the project and watch owl monkeys for the first time. We have also taught Primate Conservation Field Courses ($n=4$) where the access to radio-collared individuals has provided unparalleled opportunities for training students in data collection procedures. Finally, to celebrate the 10th anniversary of the Owl Monkey Project in 2006, we organized a visit to the monkeys and forest for national and provincial authorities, who are normally on a tight schedule. Thirty minutes were enough to find radio-collared owl monkeys even when they were sleeping at midday hidden among vines and tangles.

Discussion and Conclusions

We have provided both quantitative and qualitative evidence to evaluate the costs and benefits of using radio-collars in owl monkey research. The short-term costs of capturing and collaring individuals will determine the immediate impact on the subject, the population, the research program and the researchers. For the Owl Monkey Project, the costs to the subjects have not been significant, but the benefits to the research program have been considerable. However, we must emphasize that some of the benefits become tangible only when the project persists in time, is fully approved and supported by local authorities, and has broad community participation as well as conservation and education goals. If there are no concrete plans for a long-term presence, the removal of collars should be included in the research schedule, with adequate time allocated for this purpose toward the end of the study.

Regarding the possible immediate costs, the effects of the weight and tightness of the collar on the subject must be carefully considered (Honest and Macdonald 2003). Yet, it is difficult to decide how to proceed rationally on this matter. It is routinely accepted that the collar should not exceed 5% of the body mass of the subject, and it seems reasonable to minimize the weight of the transmitting system. However, the 5% rule ignores the fact that tolerance to a weight does not correlate linearly with body mass. Gursky (1998) evaluated the possible effects of radio-collars on tarsiers and did not find any significant differences for collars weighing between 3.1% and 7.6% of body mass. It is also necessary to evaluate carefully how tight the collar is fitted. During the initial stages of the project, we tried the radio-collars on captive owl monkeys to measure their necks and familiarize ourselves with the procedures. Nonetheless, our initial concerns for fitting the collar too tightly led us to fitting it too loosely, which most likely led to the death of 1 individual.

There was a significant impact on the social relationships between the captured individual and other group members after the temporary removal from the group. The problem arose from giving a disproportionate amount of consideration to the physical well-being of the captured individual before returning it to the forest, e.g., degree of locomotor coordination, body temperature, heart rate, in comparison to other less quantifiable parameters such as the possible impact on the social relationships with other group members. At the beginning of the study, following the protocols approved

by the Institutional Animal Care and Use Committee (IACUC), we took the captured individual to the field station for all procedures. Moreover, we sometimes delayed the return of the subject to the forest for several hours if we considered the night to be too cold or the early afternoon too hot. Despite all the training we underwent and that all procedures had been properly approved, for a few years we returned to the forest fully recovered and healthy individuals that were no longer accepted into their social groups. It is therefore essential to minimize the time the subject is removed from the group. We are now also particularly careful in choosing the time of the year for the capture, as it is during the mating season that most adult replacements take place. In conclusion, when planning to capture free-ranging individuals, the behavioral and social well-being should be considered side by side with the recommendation traditionally endorsed by veterinary doctors and IACUC committees.

There are other potential short-term costs to the individual that are more difficult to evaluate satisfactorily. The collar may influence mate choice if it increases or decreases the attractiveness of the radio-collared individual to conspecifics. The collar may increase predation risk by making the collared individual more visible, but it could also reasonably reduce predation risk if the presence of an unusual visual cue on the prey deters the predator. Finally, the collar could also affect the mobility of the individual, diminishing its ability to forage, range, escape predators, or transport dependent infants. Unfortunately, it is impossible to evaluate in the field the causal relationships between the collar and foraging ability, predation avoidance, or mating strategies. However, our observational data strongly suggest that there were no obvious immediate or dramatic effects.

Finally, an invasive procedure such as the capture of a wild primate will undoubtedly generate some reaction in at least a portion of the community where the research takes place. To most people, capturing guns or rifles do not look different from hunting weapons, and for them a 1-cc dart is larger than any bullet they have ever seen. It takes intense outreach education to help local communities understand that the procedures are relatively safe. The potential ramifications of a misunderstood procedure can have devastating effects that should not be overlooked.

Regarding the benefits, it is unquestionable that every aspect of the Owl Monkey Project would have to be modified profoundly without the use of radio-telemetry. Our research on sexual dimorphism, pair bonds, and paternal care makes the correct identification of males and females of paramount importance, something we had not been able to accomplish using natural marks. However, the fitting of radio-collars could not be justified solely for identification purposes because there are many other possible ways of marking individuals that are less intrusive and less expensive (Honest and Macdonald 2003).

Telemetry also made adequate sample sizes possible while studying a relatively small-sized arboreal forest-dwelling primate that is primarily active in dim light conditions. Radio-collaring helped us find an adequate balance between sample size and sampling intensity, a recurrent challenge in field primatology (Strier and Mendes 2009). We were able to contact several groups regularly and in short succession, effectively shortening the period of habituation as it has been reported for spider (*Ateles geoffroyi*) and capuchins (*Cebus capucinus*, Campbell and Sussman 1994). Even when we were able to habituate numerous owl monkey groups, we must indicate that the process of habituating primates is a complex one, and procedures

that have been successful with one taxon may prove inefficient with others (Williamson and Feistner 2003).

Additional benefits of using telemetry were related to our examination of dispersal, ranging, and activity patterns. The fate of dispersed individuals remains one of the least understood aspects in the life of primates. Much of our understanding of primate ranging patterns comes from the evaluation of 1 or a few groups, and researchers seldom examine the ranging of these groups simultaneously. The simultaneous monitoring of groups provided valuable information on how they avoid or attract each other while ranging in the exclusive portion of their territories or the overlapping sections of it. Simultaneous monitoring of social groups and floaters also provided us with a better understanding of the function of territoriality, mate choice, and intra- and intersexual competition. In addition, telemetry has permitted us to examine ranging patterns of strictly nocturnal owl monkeys (*Aotus vociferans*) and elusive sakis (*Pithecia aequatorialis*) in the forests of the Ecuadorian Amazonia (Di Fiore *et al.* 2007; Fernandez-Duque *et al.* 2008a, b, 2010), providing additional evidence for the benefits of radio-collars in field primatology.

Regarding activity patterns, primate field studies are often organized around dawn-to-dusk follows, regardless of the nature of the data being collected. Radio-collars offered flexibility regarding the time of the day when we could locate the groups. This allowed us to decide on a sampling schedule that was most appropriate for the question being asked. For example, when studying the influence of moonlight on owl monkey activities, we could concentrate our periods of observation during the time when the moon was high in the sky (Fernandez-Duque and Erkert 2006).

When examining our demographic data, our findings provide evidence that the fitting of radio-collars has not impacted the reproductive abilities of free-ranging owl monkeys. If anything, it is the larger groups and higher proportion of infants and juveniles in the study than in the control population that needs to be explained. A larger proportion of infants could be due to a higher birth rate, a lower infant mortality rate, or a combination of both. We think it is unlikely that the difference could be explained in terms of food availability or other environmental factors affecting birth rates differentially in the 2 areas. They are both in the same gallery forest, 10 km from each other, and there are no botanical data suggesting differences in forest composition (Placci 1995; van der Heide *et al.* 2009)

Is it possible that our presence in the forest has had a positive effect in the reproductive success of the owl monkeys through the deterrence of potential predators? We do not have adequate data on predation or predation attempts, but we have frequently witnessed interactions between tayras and raptors that strongly indicate predation risk. Infant mortality has always been relatively low in the study population (Fernandez-Duque 2007a, b), even when there were fewer researchers present for shorter periods during the initial years of the project. Therefore, we are not convinced that the observed difference in the proportion of infants and juveniles could be explained by a lower infant mortality in the focal than in the control population. The higher proportion of juveniles in the study population could be the consequence of individuals in this area dispersing at an older age. Without a longitudinal study of identified radio-collared individuals in the control groups it may not be possible to find an answer to this question. But then we would no longer have a control population.

Finally, it may be important to evaluate the extent to which the shape (as opposed to the forest structure and composition) of the 2 patches of forests could be influencing demographic processes. The control groups are located in a portion of gallery forest that is significantly narrower than the area where our study takes place (Fig. 1). A narrower forest very likely reduces the number of neighboring groups that any single group has, and it also increases the amount of edge habitat. To some extent, a narrower stretch of gallery forest may function more like an island than a wider and rounder section of the forest. Ongoing research on isolated patches of forest within the ranch and in Pilcomayo National Park will provide valuable information on the possible effects that the landscape may have on owl monkey population biology.

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