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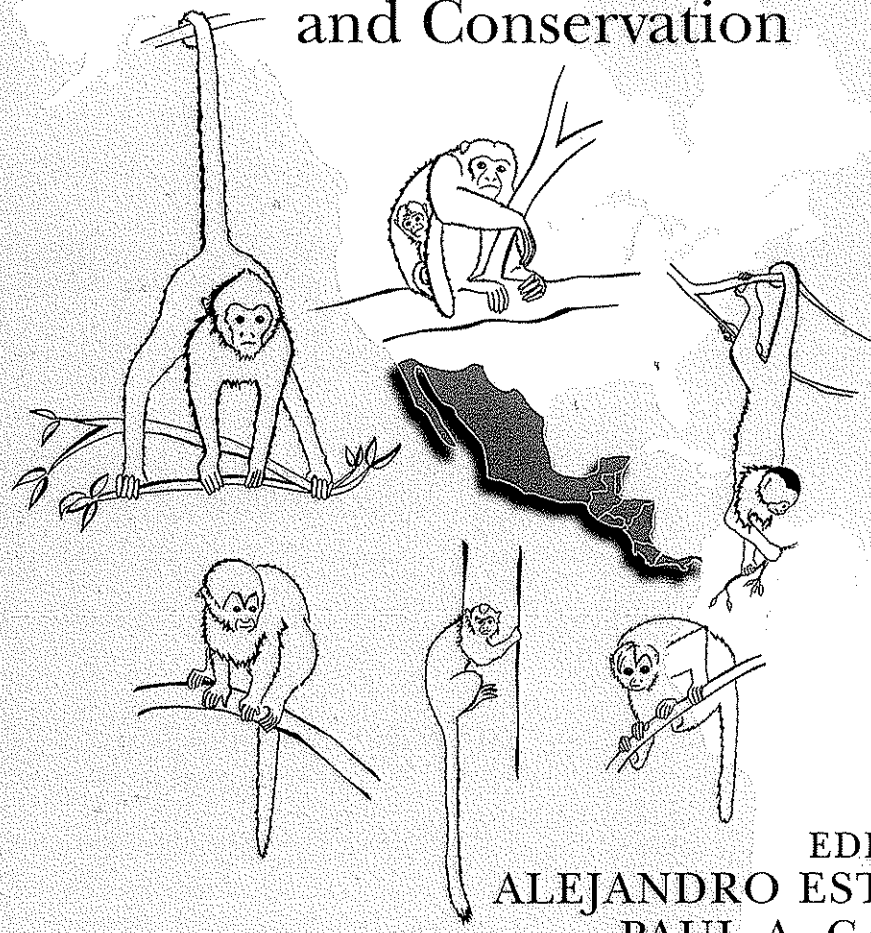
NEW PERSPECTIVES IN THE STUDY OF MESOAMERICAN PRIMATES

Distribution, Ecology, Behavior, and Conservation



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CHAPTER SEVENTEEN

Growth of a Reintroduced Spider Monkey (*Ateles geoffroyi*) Population on Barro Colorado Island, Panama

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INTRODUCTION

The release of a number of young spider monkeys (*Ateles geoffroyi*) onto Barro Colorado Island (BCI) Panama, in the early 1960s provides a unique opportunity to examine the growth of a small founder population reintroduced into a protected reserve of documented size. Increasingly, as human intervention continues to subdivide remaining large blocks of tropical forest into smaller units, the resulting fragments can be viewed as "islands," surrounded by human-modified landscapes. What rate of population growth can be predicted for spider monkeys and similar species reintroduced into suitable forest fragments? As

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will be shown, the slow expansion of this population over a period of >44 years points to the need for caution in assuming that reintroductions, even under the most fortuitous conditions, will necessarily result in the rapid repopulation of a given area. On a brighter note, though only four reproductively viable individuals survived the reintroduction, to date, the expanding population appears normal in all respects.

BACKGROUND

Barro Colorado Island is a 1600 ha protected nature reserve located in Lake Gatun, the principal water supply for the Panama Canal. The damming of the Chagras River in 1912 to create Lake Gatun flooded adjacent mainland areas. Only higher peaks and plateaus ultimately remained above water, creating islands. At present, BCI, the largest island in the lake, is densely covered in lowland tropical forest; some areas consist of old second growth, while others are made up of undisturbed primary forest estimated to be 500 or more years in age (Hubbell and Foster, 1990). Detailed descriptions of the climate and physical characteristics of BCI as well as its flora and fauna can be found in the literature (e.g. Leigh *et al.*, 1982; Milton *et al.*, 2005).

Five primate species occur naturally in this area of Panama. Founder populations of three of these species (i.e. *Alouatta palliata*, *Saguinus geoffroyi*, *Cebus capucinus*) and possibly four (*Aotus zonalis*) were trapped on what became BCI by the rising lake water and their descendents can be found on the island to this day. Though black-handed spider monkeys (*A. geoffroyi*) are also native to this region of Panama, by 1912, they had been entirely extirpated from the area by hunters and none remained to populate BCI.

Initial Reintroduction

Beginning in December 1959 and continuing intermittently until mid-1966, the then-Director of the Smithsonian Tropical Research Institute (STRI) in Panama, the late Martin Monihan, began to release immature A. *geoffroyi* onto BCI. It was hoped that the young monkeys would survive and lead to the re-establishment of a free-ranging spider monkey population.

At the time of the reintroduction effort, it was common to find young monkeys of various species routinely offered for sale in the public market in Panama City. The usual way to secure a young monkey for the pet trade is to shoot the mother and remove the clinging, dependent young infant from her body. Thus,

it is highly probable that all of the immature spider monkeys purchased for release onto BCI were tiny dependent infants at the time of their initial capture. Some likely were kept as pets for shorter or longer periods of time before being offered for sale and brought to BCI. Given the usual banana-dominated diet offered to captive monkeys in Panama, most young monkeys likely were not in optimal physical condition at the time of purchase.

The exact number of spider monkeys released onto BCI is not known (Dare, 1974). Conversations with the BCI caretaker for the young monkeys, the late Bonifacio de Leon, indicate that 18 or more monkeys were ultimately released. Their estimated ages ranged from perhaps 1 year to 3 or 4 years (Dare, 1974). Some were released near the laboratory clearing on the northeastern side of BCI while others were released at more distant locales (B. de Leon, pers. comm.). All were offered fresh fruits and other foods each day on feeding platforms constructed in each release area as the monkeys were viewed as far too young and/or inexperienced to forage successfully in the BCI forest. This provisioning was gradually ended as the young monkeys matured and became more self-sufficient at finding wild foods.

Even with nutritional supplementation, most monkeys did not survive the reintroduction. Data indicate that by the mid-1960s, only five (one male and four females) of the released monkeys were still alive (Eisenberg and Kuhen, 1966; Richard, 1970). The single male survivor, Chombo, was estimated to be 3–4 years old at the time of his release on BCI in late December 1959 (Dare, 1974). Three or all four of the surviving females were released onto BCI in 1960; at the time of their release, three were estimated to be one to one and one-half years old and the fourth was estimated to be 3 years old (Dare, 1974). There is mention of a fifth female possibly released on BCI between 1965 and 1966 at an estimated age of 3 years (Dare, 1974). This fifth female may have died shortly thereafter or one of the original 1960-introduced females may have died as various observers on BCI in the mid-to-late 1960s consistently report only five adults (one male and four females; Eisenberg and Kuhen, 1966; Richard, 1970). One of the four surviving females (KH) appears to have been barren. Though Dare (1974) mentions a possible birth by this female in 1969, in KM's experience (from March 1974 to this female's death at some point in 1989), this female was never noted with an infant.

An accurate record of the BCI spider monkey population in terms of the timing and number of births, the identity of the mother in each case and the timing and number of deaths can never be provided since no one collected the necessary continuous long-term data. In spite of this, as shown in Table 1,

Table 1. Censuses of BCI spider monkey population, 1964–2003

Year	Adult M	Adult F	Juv M	Juv F	Total Juv	Infant M	Infant F	Total infant	Total adult	Total immatures	Total	Obser.
1964	0	0	1	4	5	0	0	0	0	5	5	E & K
1966	1	4	0	0	0	1	2	3	5	3	8	E & K, Dare
1968	1	4	0	0	0	2	2	4	5	4	9	Richard
1970	1	4	1	1	2	2	0	2	5	8	13	Dare
1972	3	5	4	0	4	2	2	4	8	8	16	Dare
1974	5	4	1	2	3	1	1	2	9	5	14	KM
1978	4	4	1	2	3	2	0	2	8	5	13	KM
1979	4	4	1	2	3	3	1	4	8	7	15	KM, Glanz
1980	3	5	2	1	3	1	1	2	8	5	13	KM
1981	3	5	2	1	3	1	2	3	8	6	14	KM
1983	3	6	2	2	4	1–2	0–1	2	9	6	15	KM
1984	4	6	1	0	1	1	2	3	10	4	14	KM
1985	4	4	1	1	2	2	3	5	8	7	15	KM
1986	3	5	1	3	4	1	3	4	8	8	16	KM
1987	3	5	1	3	4	1	3	4	8	8	16	KM
1988	3	5	1	3	4	1	2	3	8	7	15	KM
1989	4	5	1	2	3	1	2	3	9	6	15	Ahumada
1990	3	5	1	2	3	1	2	3	8	6	14	KM
1991	5	5	2	3	5	2	1	3	10	8	18	KM
1995	6	4	1	5	6	1	2	3	10	9	19	KM
1997	5	6	2	7	9	0	1	1	11	10	21	Campbell
1998	4	7	1	6	7	0	2	2	11	9	20	Campbell
1999	4	8	1	6	7	5	3	8	12	15	27	Campbell
2001	4	10			7			6	14	13	27	KM
2002	3	9			8			7	12	15	27	KM
2003	4	10			7			7	14	14	28	KM

sufficient observational records exist such that a reasonable overview of the growth of this founder population can in fact be provided.

GROWTH OF THE POPULATION

Reproductive maturity for wild female spider monkeys on BCI is placed at ≥6.5 years (Milton, 1981). Therefore, 3–5 years had to pass for any of the surviving founder females to reach reproductive maturity. The first mention of spider monkey infants born on BCI comes from Eisenberg and Kuhen (1966), who noted the presence of three infant spider monkeys in the spring of 1966. There is strong general consensus that these were the first spider monkey infants born on BCI.

As Chombo was the only male to survive the reintroduction, it is certain that he fathered *all* infants born between 1959 and 1971 (by which time at least one F1 male could have reached reproductive maturity). As the dominant male, Chombo may have continued to father most or all infants born on BCI until his death in 1978, at an estimated age of 22 years.

After the three confirmed births in 1966, the birth record becomes blurred until around 1972. Data suggest that some 9–11 infants may have been born between 1966 and 1972 (Dare, 1974). Though various "spider monkey births" are noted in the BCI record books over this period, these record books were casual accounts of events noted by island visitors and cannot be relied on in terms of accuracy. Given the 28–36 month interbirth interval characteristic of wild spider monkeys (Milton, 1981; Symington, 1988), some of these "birth" records are likely redundant. Young spider monkeys are deceptively neonatal such that human observers not familiar with their growth trajectory invariably greatly underestimate their actual age.

In 1972, a USA graduate student, Ron Dare, came to BCI to carry out a study of spider monkey behavior for his doctoral dissertation. He created a photographic record for each individual, finding a total of 13 spider monkeys at the start (March 1972) of his study and 15 at the conclusion (December 1972). During his study, one adult F1 male died (born in 1966) and three infants (one male and two females) were born (Dare, 1974).

In March 1974, KM came to BCI to carry out fieldwork on the howler monkey (*A. palliata*) population and began to note down occasional information on the spider monkeys as well; in 1978–1979, she collected feeding and ranging data on the spider monkey population (Milton, 1993). By late 1974, there

was a total of 14 spider monkeys on BCI—five clearly recognizable as the original founders and nine F1 offspring. These latter included four subadult to adult males, two juvenile females, one juvenile male and two infants, a male and a female, both born in 1974. A female infant was born in 1975, and two male infants were born in 1977. Another male infant as well as the first F2 generation infant, a female, were born in 1979. If all of these individuals had lived, this should have given a population of ≥19 spider monkeys on BCI by late 1979. However, during this same period, the founder male and one juvenile male had died, one founder female had to be sacrificed for a rabies test and her infant daughter was later sent to a US zoo. A December 1979 census showed a total of only 15 individuals (Milton, pers.obs.; see also Glanz, 1982).

After 1979, KM no longer lived on BCI but tried to census the BCI spider monkey population whenever she visited the island—generally at least once in a year. Though often able to count what appeared to be the total spider monkey population, by the mid-1980s, she was unable to distinguish younger members as individuals and her counts surely missed some births and deaths.

In 1988, a Colombian undergraduate student, Jorge Ahumada, came to BCI to study grooming behavior in *Ateles*. Ahumada provided accurate identification for each spider monkey present in the population during his stay on the island and KM attempted to link her identifications of older individuals with his. The same 15 individuals were alive at both the start (October 1988) and conclusion of his study (January 1989; Ahumada, 1992). On KM's visits to BCI, she continued to try and census the spider monkey population whenever the opportunity presented itself.

In fall 1997, a graduate student from the USA, Christina Campbell, came to BCI to carry out a dissertation study of reproductive behavior in spider monkeys. Like Ahumada, she described each member of the population. By 1997, too much time had passed for KM to be able to link her and Ahumada's identification records to Campbell's 1997 identity data (Campbell, 2000). Campbell found a total of 21 spider monkeys on BCI at the start of her study (August 1997) and 20 at the conclusion (August 1998). There were various changes in group composition during her study—three individuals died (one adult male, one juvenile male, and one new infant of undetermined sex) and two infants were born (both female).

Thus, overall, there are a series of accurate "touchstone" censuses of all spider monkeys on BCI, each described and known as an individual, for the particular

years in which detailed observations were being carried out by one or another spider monkey researcher. Then, there are a number of opportunistic censuses that often lack individual identification. A summary of all available census data is presented in Table 1.

Pattern of Growth

Census data over the period 1960–2003 show that once the population grew to a size of around 14–16 animals in the early 1970s, it then hit what might be described as a long plateau in terms of any consistent population growth for almost three decades (Figure 1). The population was not in stasis during this period—data indicate the birth of new individuals and the disappearance and presumed death of others. For example, in 1984, one of the three remaining founder females (Freckles) died at an estimated age of 24 years; in 1987 another founder female (Blackie) died at an estimated age of 27 years. Both females continued to produce offspring until they disappeared. The barren female (KH), the only remaining member of the original cohort, died in 1989 at an estimated age of 26 years. There were always infants and juveniles present in the population. But it seems certain that between 1972 when Dare left BCI and 1998 when Campbell left BCI, a period of almost 26 years, the population had increased by only three individuals (Table 1 and Figure 1).

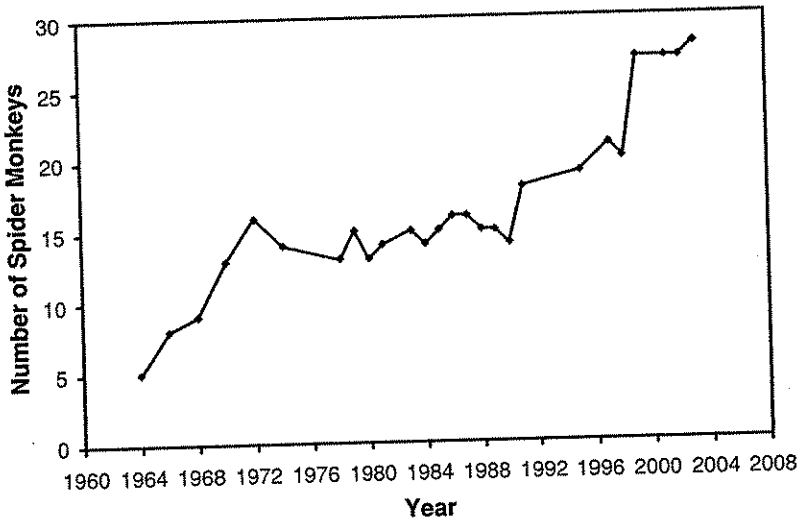

Figure 1. Growth of the BCI spider monkey population, 1964–2003.

The nature of exponential growth is well appreciated. Founder populations tend to grow slowly initially and then, if they persist, there is typically a sharp upward growth trajectory. It would seem that by the new millennium, the BCI spider monkey population had finally turned the corner and begun to accelerate notably in terms of size. In 1997, Campbell counted 21 spider monkeys; but by 1999, there was a total of 27 as six infants were born in 1999 (Campbell, 2000). KM counted 27 spider monkeys in 2001 and 2002 and 28 in 2003. Therefore, over the approximately 44-year period (1960–2003) since the initial reintroduction effort, overall population size has increased almost six-fold (from an initial size of five individuals to a current size of 28), an increase of around 4% per year.

Population Model

An age-based population growth model was generated using the program MATLAB 7 (MathWorks, 2004) in order to approximate the observed growth curve of the BCI spider monkey population (Figure 2). The model begins with one male and three breeding females, and assumes that the fourth female had no offspring. Each female is allowed to give birth every 36 months and age at sexual maturity for females is placed at 7 years. The sex ratio of male and female

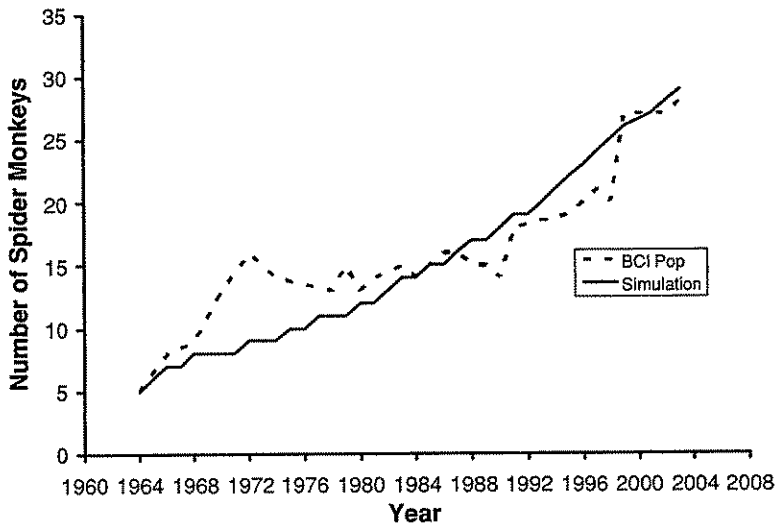

Figure 2. Comparison of simulated and observed growth for BCI spider monkey population.

births is assumed to be equal. These reproductive parameters were derived from estimated pedigrees for this population.

The population growth rate, as well as the numbers of individuals in each age/sex class was then simulated for 40 years according to different survivorship values. Simulated population growth was most sensitive to varying levels of adult female survivorship. Even with all other parameters set at 100% survivorship, adult female survivorship from year to year has to be above 90% in order for the population to reach current levels. The best-fit curve which approximates observed population trends on BCI contains modest mortality values (i.e. large survivorship rates) for all age-sex classes except for juvenile males approaching adulthood. Adult females have a survivorship probability between 98% and 99% per year. Male and female infants were given a fairly large survivorship probability of 75% per year. Male and female juveniles were given a survivorship probability of 90% per year, with one exception: the probability of a male juvenile spider monkey transitioning to an adult male spider monkey was lowered to 50% per year. These values yielded simulated population demographics that are very similar to those present on BCI today (2003): 29 individuals total, 4 males, 11 females, and 14 juveniles and infants (Figure 3).

However, while this simulation can illustrate the average reproductive rates and survivorship rates for various age/sex classes within the spider monkey

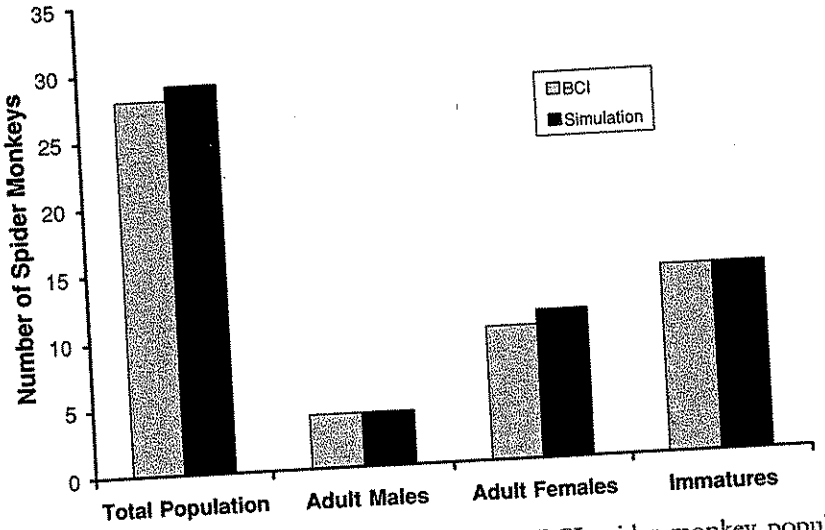

Figure 3. Comparison of simulated and observed BCI spider monkey population demographics in 2003.

population over the last 40 years, it cannot approximate the variation (i.e. population increases and decreases over short periods of time) that occurs between the starting and ending points (see Figure 2). This variation could result from a number of factors, including biased sex ratios, census errors, or human intervention (such as the removal of a breeding female and her daughter from the population in the 1970s). It is of interest to note that if 100% survivorship is assumed for all age/sex classes, given the BCI reproductive parameters, the BCI population should have grown to ≥170 individuals by now. In fact, it is less than 30 individuals (Table 1).

NATAL SEX RATIO

Some data suggest that spider monkeys may be able to bias the sex of their infants (Symington, 1987). In Peru, a 5-year birth record showed that significantly more female infants (32) were born than male infants (12) (Symington, 1987). It was suggested that at this site, lower-ranking females tended to produce daughters almost exclusively, while higher-ranking females biased their investment somewhat less strongly toward sons (Symington, 1987). At this Peruvian site, over the 5-year period, 21 out of 21 infants produced by low-ranking females were female while high-ranking females produced 12 male and 11 female infants (Symington, 1987). In contrast to the Peruvian situation, birth records for BCI (which are not complete but which should not show observer bias) suggest a natal sex ratio of approximately 1:1. However, it is the case that over the first reproductive decade, a disproportionate number of the F1 generation on BCI were male. Dare's (1974) data show that, in 1973, there were seven F1 male spider monkeys alive on BCI and only two F1 females—these in addition to the five original founders. The lack of maturing young females certainly contributed to the slow initial growth of the population. Also, as mentioned above, in late 1975, one founder female had to be sacrificed for a rabies test and her infant daughter was later shipped to a zoo in the USA. The human-mediated loss of these two females likewise had a negative impact on initial population growth.

At present, there are an unprecedented number of adult female spider monkeys on BCI (Table 1). Campbell (2000) noted that, of the six 1999 births, five were female and only one was male. Perhaps there is finally a sufficient cohort of reproductively active female spider monkeys on BCI to have high-ranking

and low-ranking female status. Further observation of the natal sex ratio over the next decade or so will help to test this possibility.

ADULT SEX RATIO

Though overall data suggest a natal sex ratio of approximately 1:1 for the BCI spider monkey population, it is certain that, initially, male infants outnumbered female infants. Available data suggest that most of the initial F1 males survived in the 1970s. Both sexes can live upto >20 years of age (Milton, 1981). Yet, there never seems to have been a time when more than six and typically three or four adult males were present in the population together. Even today with some 10 adult females in the population, there are only 4 adult males (M:F adult sex ratio = 1:2.5).

It is the case that there tend to be more adult females than males in spider monkey groups. Klein and Klein (1977) reported that the two study groups of *Ateles belzebuth* they worked with at La Macarena, Colombia, were composed of 5 adult males and 12 adult females (1:2.4) and 3 adult males and 11 adult females (1:3.5), respectively. Decades later, Shimooka (2003) likewise reported 5 adult males and 10–11 adult females in his study group of *A. belzebuth* at La Macarena. Symington's two *Ateles paniscus* communities in Peru showed the same pattern—the East community had 7 adult males and 13 adult females, while the Lake community had 6 adult males and 11 adult females—an overall total of 13 adult males and 24 adult females and an adult sex ratio of approximately 1:2 (Symington, 1986, 1987, 1988). Similar female-biased adult sex ratios have been reported for spider monkey groups at various other sites (Campbell, 2000). The BCI data, which consistently show no more than three to six fully adult males present at any given time, indicate that the normative number of adult males per group for *Ateles* spp. (i.e. 3–6 males per group), is somehow maintained regardless of total group size or the number of adult females in it (Table 1).

CAN BCI SUPPORT MORE THAN ONE GROUP?

Barro Colorado Island seems sufficiently large and productive to support more than a single spider monkey group, though this is only conjecture. In the late 1970s, KM estimated that some members of the BCI spider monkey population,

which then consisted of some 14–15 individuals, might range over an area as large as 800 ha (Milton, 1981). In 1998, Campbell (2000) estimated that that the 20–21 BCI spider monkeys she observed were using an area of some 960 ha. At present, there are some 28 spider monkeys in total on BCI yielding a density of 0.017 spider monkeys per hectare. Symington's (1987) two groups in Peru ranged over home range areas estimated at only 150–250 ha (375 ha for both communities together, 52 monkeys total for both communities yielding a density of 0.138 spider monkey per ha). Campbell (2000) noted that the density of spider monkeys on BCI was much lower than that recorded for various other sites.

As BCI is an island, there is a large edge effect as well as several narrow peninsulas. Island topography may reduce suitable habitat such that only a single spider monkey group can be supported due to the need of its members to range over a large portion of the 1600 ha island to encounter sufficient high quality food throughout the year. During the late rainy–early dry season on BCI, spider monkeys appear nutritionally stressed (Milton, 1981; unpublished data), suggesting that sufficient suitable food may at times be scarce.

It will be interesting to follow the growth trajectory of the population now that it has reached a size commensurate with many spider monkey groups (communities) elsewhere. If the adult females on BCI continue to produce new infants approximately every 3 years, with approximately 10 adult females now present, all else being equal, a considerable increase in spider monkey numbers seems possible over the next decade.

BOTTLENECK EFFECT AND ESTIMATED HETEROZYGOSITY

As there was only a single founder male, his Y chromosome is and always has been the only Y chromosome available on BCI. For the first 10 or so years after reintroduction, the founder male, therefore, must have fathered all infants, male and female. This means that at sexual maturity, the first few female members of the F1 generation could mate only with their father (who died in 1978) or a half- or full sib. However, even though the BCI spider monkey population can be said to have passed through a decided founder bottleneck, contrary to what might seem inevitable, this does not mean that average heterozygosity fell to dangerously low levels (Nei *et al.*, 1975).

There are no data to suggest that any of the breeding founders were related. Therefore, one unrelated male and three (or initially, possibly four) unrelated

females provided the initial gene pool. In the wild, one generally finds three to six adult males per group, but because males of this genus are philopatric, all males of a given group may be close kin. The most dominant male may also have the highest reproductive success. The initial BCI situation with only a single male clearly lacks the genetic scope provided by four or five adult males, even if all are close kin. But as most or all males in mainland groups may be related and one male in particular may sire a high percentage of infants at any one time, over the short term, the BCI situation actually may not be as peculiar as it first appears. Wild spider monkey groups elsewhere typically have more than three to four reproductively active adult females but, similar to the initial BCI situation, these females likely are not related as in the genus *Ateles*, juvenile females disperse from their natal groups (Symington, 1987). However, unlike mainland groups, there was no way for new genetic material to enter the BCI population except through mutations as no gene flow was possible.

What level of heterozygosity may have been lost in the founder event? Inbreeding and loss of genetic diversity are an inevitable consequence of small population size (Wayne *et al.*, 1991; Bouzat *et al.*, 1998). Although the BCI spider monkey population began with one male and four females, the effective population size of the founder population was likely reduced by two factors: (1) one of the females is presumed to be barren at the time of introduction, and (2) all females had to mate with the same male (i.e. the assumption of random mating is somewhat violated by a biased sex ratio). Once these two factors are taken into account, the effective population size of the BCI founders becomes three individuals:

$$N_e = \frac{4\,N_{ef}\,N_{em}}{(N_{ef} + N_{em})} \qquad (1)$$

where

N_e = Effective population size
N_{ef} = No. females
N_{em} = No. males

This unequal sex ratio of breeding males and females has continued throughout the subsequent generations of spider monkey populations, and all of the calculations involved in the subsequent assessments of inbreeding adjust for this factor.

Although the reduction of a population to an effective size of three individuals is a drastic decrease in population size, the immediate impact of

this bottleneck on population genetic diversity (as measured by average heterozygosity) is relatively small. Estimates indicate that the BCI spider monkey population immediately after placement on BCI likely retained approximately 83.3% of the heterozygosity present within a mainland randomly mating population:

$$\frac{H_1}{H_0} = 1 - \left(\frac{1}{2N_e}\right) \tag{2}$$

where

H_1 = Heterozygosity immediately after the bottleneck
H_0 = Heterozygosity before bottleneck
N_e = effective population size

However, sustained reductions in population size after a bottleneck, such as that which has occurred on BCI, can substantially reduce average heterozygosity and allele frequencies within a population over time (Nei *et al.*, 1975; Frankham *et al.*, 2002). In the small closed population of spider monkeys on BCI, inbreeding is unavoidable as all individuals become related by descent. A common measure of this effect is the inbreeding coefficient (F_t) which measures the probability that an individual in a given generation (t) will receive identical alleles from both parents due to common descent:

$$F_t = 1 - \prod_{i=1}^{t}\left[1 - \frac{1}{2N_{ei}}\right] \tag{3}$$

where

F_t = Inbreeding coefficient at generation t
N_{ei} = Effective population size in the ith generation

All equations above are taked from Frankham *et al.*, 2002.

Due to an inability to construct a complete pedigree for the BCI spider monkey population, it is impossible to calculate an exact inbreeding coefficient in the absence of genetic data. However, from the partial pedigree reconstructed between 1966 and 2003, we can garner approximate estimations of the effective population size in each generation, thereby allowing the calculation of a conservative approximation of the inbreeding coefficient for the current generation. For example, from census data, we can confirm that there were at least nine breeding F1 adults present in the population at various times. If we assume that each successive generation yields at least as many individuals as the founding population (a conservative assumption given that the F1 generation was at least

three times the size of the founding population), the youngest generation of breeding spider monkeys on BCI would have an estimated inbreeding coefficient of approximately 0.338. This value indicates that approximately 66.2% of the average heterozygosity of a mainland population remains on BCI, given the population growth trend over the past 40 years ($H_1/H_0 = 1 - F_t$; Frankham *et al.*, 2002). Yet, given the properties of Equation (3), as the effective population size on BCI continues to increase, the corresponding decrease in average heterozygosity becomes negligible. For example, if the effective population size of the next generation is 14 individuals (the current number of breeding adults in the population), the corresponding decrease in average heterozygosity would only be approximately 4%.

NOISE

Two other features of spider monkey population dynamics on BCI require mention, i.e. racetrack monkeys and small island monkeys.

Racetrack Monkeys

In April 1991, STRI permitted the release of five spider monkeys, apparently all *A. geoffroyi*, onto BCI. These monkeys were released at the end of Armour trail—an area of old growth forest on the extreme south-western side of the island, largely removed from the normal ranging circumference of the resident spider monkey population. The five racetrack monkeys were of various ages and apparently consisted of one male and four females. They had been captive animals, exhibited in a cage at the public racetrack in Panama City for the amusement of its patrons. For some unknown reason, possibly to enhance genetic diversity of the resident spider monkey population, STRI decided to permit the release of these racetrack monkeys onto BCI. To our knowledge, no study was carried out to determine the parasite loads, possible health problems or other features of the racetrack monkeys—features that should have been evaluated prior to permitting the release of these monkeys into a protected nature reserve—one that now had a viable spider monkey population of its own as well as viable populations of three or four other primate species. At least one juvenile female from the racetrack cohort had no teeth—so it is not clear how she was expected to survive her new freedom in the forest.

Data suggest that none of the racetrack spider monkeys survived. KM and several colleagues, a veterinarian and two researchers from the Primate Center

at U.C. Davis, arrived on BCI the day after the release and spent several days working with howler monkeys in the release area. After their departure, KM remained on BCI for several more weeks, often working in the Armour release area. During that entire period, she noted nothing unusual in the resident spider monkey population nor did she hear any outbursts of spider monkey vocalizations in the forest that might suggest any newcomers had met the residents. The amount of noise that a group of excited spider monkeys can make is extreme and such noise carries clearly over a long distance in the forest (KM, pers. obs.). We hypothesize that the racetrack monkeys starved due to their inexperience in finding wild foods. They were probably also in poor physical condition at the time of release. KM later recovered the skulls of two spider monkeys in the release area (including the toothless juvenile) but the fate of the other three individuals is not known.

Small Island Monkeys

Occasionally, there are reports of black-handed spider monkeys sighted on one or another of the smaller islands adjacent to BCI. It has been speculated that people with boats may at times release unwanted pet monkeys onto smaller islands in Lake Gatun, which could be the source of some or all of these individuals. In June 2004, we and various colleagues saw an adult male spider monkey and a female spider monkey, both apparently in excellent condition, on Orchid Island, a small forested island directly adjacent to BCI. These two individuals may have swum the short distance from BCI to Orchid Island. The factor or factors that would induce spider monkeys to enter the caiman-infested lake and swim to Orchid Island are not known. The forest on Orchid Island is far less diverse than that on BCI (KM, pers. obs.). Both of the Orchid Island animals appeared to be young adults; they were not at all tame, suggesting that they were not former pets or, if so, did not retain fond memories of past human interactions. Perhaps these two individuals voluntarily emigrated from BCI in search of new habitat.

Campbell (2000) reported that one female spider monkey, known to her as an individual and initially seen on a small island adjacent to BCI, was later seen on BCI with the BCI spider monkey group, suggesting that some spider monkeys may swim between BCI and nearby islands. This remains to be confirmed as, to date, there have been no observations of spider monkeys swimming in Lake Gatun.

Future genetic studies may indicate whether any of the racetrack monkeys were incorporated into the resident population on BCI and also help to resolve the possible origins of spider monkeys occasionally sighted on nearby islands. If the racetrack monkeys perished, all individuals on BCI should be the descendents of the few initial founders. Conversely, if one or more of the racetrack monkeys survived, they may have provided new genetic input to the resident population. Genetic study will also provide an actual inbreeding coefficient that can be compared with the above estimate as well as with those of mainland spider monkey populations elsewhere. Such data should be of interest to conservation biologists for it will help to answer questions related to minimum size and composition thresholds for similar reintroduction efforts.

SUMMARY

The present-day BCI spider monkey population on Barro Colorado Island, Republic of Panama, results from the reintroduction of ≥19 young spider monkeys onto the island in the early 1960s. One male and four females survived the reintroduction though one of these females apparently was barren. No data suggest that any of the five founder individuals were related. The first three F1 infants were born in early 1966. By late 1974, there was a total of 14 spider monkeys on BCI—five clearly recognizable as the original founders and nine F1 offspring. These latter included four subadult to adult males, two juvenile females, one juvenile male and two infants, a male and a female, both born in 1974. Thus, a preponderance of the initial surviving members of the F1 generation was male. Over the next 25 or so years, little change was noted in the size of the BCI spider monkey population. Though births and deaths were recorded, the overall size of the population remained approximately the same (14–16 individuals). Only in the late 1990s did the BCI spider monkey population appear to turn the corner and begin to accelerate notably in terms of size. In 1997, there was an estimated total of 20 spider monkeys on BCI and by 1999, this number had increased to 27 (Campbell 2000). The composition and size of the present-day BCI spider monkey population now approximates those of various other wild spider monkey populations elsewhere.

It may seem surprising that a population originating from such a small number of founders could survive and grow successfully over time as this one has done without manifesting any inbreeding or behavioral problems. To date, however, the picture emerging from BCI suggests that, given suitable

protected habitat and nutritional supplementation in the early stages of the founder event, even a small number of unrelated young animals as socially and ecologically complex as spider monkeys can reach successful reproductive adulthood without adult role models or further human intervention and then continue on successfully as a viable breeding population into the indefinite future.

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