RESEARCH ARTICLES

Dispersal by *Propithecus verreauxi* at Beza Mahafaly, Madagascar: 1984–1991

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From 1984 to 1991, 126 males and females were marked and monitored in a wild population of *Propithecus verreauxi* in southwest Madagascar. Animals were assigned birth years, based on known birth date or degree of dental wear calibrated by recapture data. Twenty-one of 27 groups identified in 1984 persisted within stable home range boundaries, 6 groups disappeared, and 6 new groups formed. Only males transferred between existing groups, although individuals of both sexes left groups to form new groups. The home range of the group into which a male transferred usually overlapped that of his group of origin. On average, 35% of males aged 3–6 years transferred each year. Older males transferred at a lower rate. Three to 6-year-old males were more likely than older males to transfer two or three times. Most 3–6-year old males transferred into groups with a higher proportion and number of females, whereas older males were progressively more likely to transfer into groups with a lower proportion and number of females. New groups were formed by older males, whose mates had died or who had not been successful in joining an existing group, and by young, nulliparous females. Males have rarely been observed for more than 5 years in the same group. Dispersal by 3–6-year-old males appeared to be voluntary. Females helped evict non-natal males from the group but did not prevent new males from joining. Age at first reproduction was 5 years in this population. Forced secondary dispersal may occur when maturing females cease to tolerate males who may be their fathers.
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INTRODUCTION

Dispersal, the movement of an individual from its site or group of origin to its first or subsequent breeding site or group [Shields, 1987], characterizes one or both sexes in all species of mammals [Gaines & McClenaghan, 1980; Greenwood, 1980]. However, the growing body of data on dispersal is more striking for the complexity it reveals than for its ability to explain the phenomenon [Chepko-Sade & Halpin, 1987]. Individuals disperse over different distances, with different proximate

causes at different times in their lives, and the genetic, ecological, and behavioral consequences are diverse [Clutton-Brock, 1989; Henzi & Lawes, 1988; Holekamp & Sherman 1989; Lidicker & Patton 1987; Melnick & Pearl, 1987; Moore, 1984; Mech, 1987; Packer, 1979; Pusey, 1980; Rood, 1987; Shields, 1988; Waser & Jones, 1983; Waser, 1988; Wood et al., 1985]. In primates, intrasexual competition for mates and inbreeding avoidance are most commonly proposed to account for natal and secondary dispersal [Moore and Ali, 1984; Pusey and Packer, 1987]. Evaluating these explanations requires a knowledge of behavior, life history patterns, and genetic relationships difficult to obtain for primates in the wild, and field experiments are rarely feasible or desirable to test hypotheses directly [c.f. Ligon & Ligon, 1988; Zack & Rabenold, 1989]. As a result, our understanding of primate dispersal is still far from complete.

In the sifaka (*Propithecus verreauxi*), a large diurnal and folivorous primate endemic to Madagascar, populations are divided into many small groups containing females presumed to be matrilineally related, along with natal and non-natal males. The total and proportionate number of males and females in these groups is quite variable in space and time [Richard, 1985]. The sifaka mating system is not well documented, but mating by visiting males from other groups has been reported as well as mating by males resident in the group, during the brief annual breeding season [Richard, 1974, 1992] (O'Connor, personal communication). Dispersal by male sifakas typically takes the form of intergroup transfer and it has been suggested that this, together with frequent intergroup encounters, visits by males, and mating by non-group males, links groups into socioreproductively significant "neighborhoods" [Jolly, 1966; Richard, 1978, 1985]. However, although transfer by males is common and a male may transfer more than once in his lifetime, neither the spatial patterning of transfer within the population nor its timing and frequency in the context of male life histories have been studied. Dispersal by female sifakas is rare. There are occasional reports of female transfer or of females forming new groups with new males [e.g., Jolly, 1966; Jolly et al., 1982], but the circumstances under which this occurs are poorly documented.

We present the results of a 7 year study of dispersal in the sifaka population at Beza Mahafaly in southwest Madagascar, 126 members of which have been marked. We focus on the "careers" [van Noordwijk & van Schaik, 1988] of the longest-studied animals and on the groups to which they belonged or which they founded: 52 marked males censused for 226 male-years and 37 marked females censused for 106 female-years, distributed among 33 social groups. The first subsection under Results below describes the history of group persistence, disintegration, and formation between 1984 and 1989. This history has important implications for dispersal, by establishing the nature of the social landscape and the reproductive opportunities encountered by animals seeking to transfer. The second subsection describes patterns of dispersal between 1984 and 1991, including rates of transfer by males of different ages, the distance over which they transfer, the composition of the groups into which they transfer compared to those from which they came, the tenure of their stay in groups, and the founding of new groups by males and females. Finally, the third subsection under Results considers the behavioral context of transfer, using observations of four focal groups carried out in 1984–85.

We include limited as well as long-distance movements in the term dispersal [Waser and Jones, 1983] and regard transfer between groups as a mode of dispersal, the one most common in this species. We distinguish between *natal dispersal,* the movement of an individual out of the group in which it was born, and *secondary dispersal,* which includes episodes of dispersal thereafter [Rood, 1987].

Group of origin refers to the group in which a male was first identified. For many 3–6-year-old males, the group of origin was also known to be the *natal group*.

Our findings provide support for the concept of a neighborhood in sifakas. However, they also suggest that previous characterizations of sifaka social groups as being of little or no significance as reproductive units were overdrawn. We argue that both intrasexual competition and inbreeding avoidance shape natal and secondary dispersal patterns; the relative importance of these determinants and the kinds of dispersal events they trigger are conditioned by a male's age, mating history, and the local demographic context.

STUDY SITE, SUBJECTS, AND METHODS

The Beza Mahafaly Special Reserve consists of two small protected areas within a much larger but unprotected forest in southwest Madagascar (Fig. 1). The reserve was established with integrated conservation and development goals [see Rakotomanga et al., 1987; Richard et al., 1987], and is the site of several ongoing studies [e.g., Sussman, 1991; Sauther, 1991]. The climate is highly seasonal in this region of Madagascar, and the forest at Beza Mahafaly includes a gradient from xerophytic vegetation to a narrow strip of riverine forest dominated by *Tamarindus indica*. With increasing distance from the river, xerophytic plant-forms replace the riverine vegetation. *Lemur catta* is abundant in the reserve, as are two nocturnal primate species, *Lepilemur mustelinus leucopus* and *Microcebus murinus*. There is a diverse fauna of other mammals, birds, reptiles, and insects [Richard et al., 1987].

The study population was defined by the boundaries of Sector 1 of the reserve (variously a river bed and a fence to keep out cattle), which comprises about 80 ha of riverine and transitional forest. In 1984, the population consisted of some 175 individuals living in 27 social groups with overlapping home ranges averaging 4 ha, which lay partly or completely within the boundaries of Sector 1 of the reserve. The study population was part of a larger biological population [cf. Caughley, 1977], and animals moved freely between the reserve and the contiguous forest.

Between November 1984 and August 1991, 126 animals from the study population were captured, given collars and numbered tags, and released. Biometric measures and estimates of age were obtained for this subset of the study population. Natural markings were used to identify other animals whenever possible. Five age classes (A–E) were initially established [Richard et al., 1991], representing a range from no toothwear to extreme wear, ascertained from casts made from impressions taken of the upper dentition. Eight animals were recaptured after intervals of 3–5 years, two each from animals assigned to age classes A–D at the time of first capture. This enabled us to calibrate rates of dental wear, to estimate the number of years represented by each age class, and to assign each individual an estimated birth year. The estimated age of an animal in *the month of July preceding the event described* is shown in parentheses after its identification number (see Table I). July was chosen to standardize ages because births occur in an approximately 6 week period each year, between early June and late August. Additional information about methods of capturing animals and estimating age from toothwear is given elsewhere [Richard et al., 1991].

Our data come from annual censuses, ad hoc observations of group composition at other times of year, and a detailed study of four social groups carried out between November 1984 and May 1985. We began collecting data on the study population in October 1984, and complete censuses have been carried out each year over a 4 week period in June/July (1985, 1986, 1987, 1988) and August (1989, 1990, 1991), by walking slowly along a grid of trails running north-south and east-west
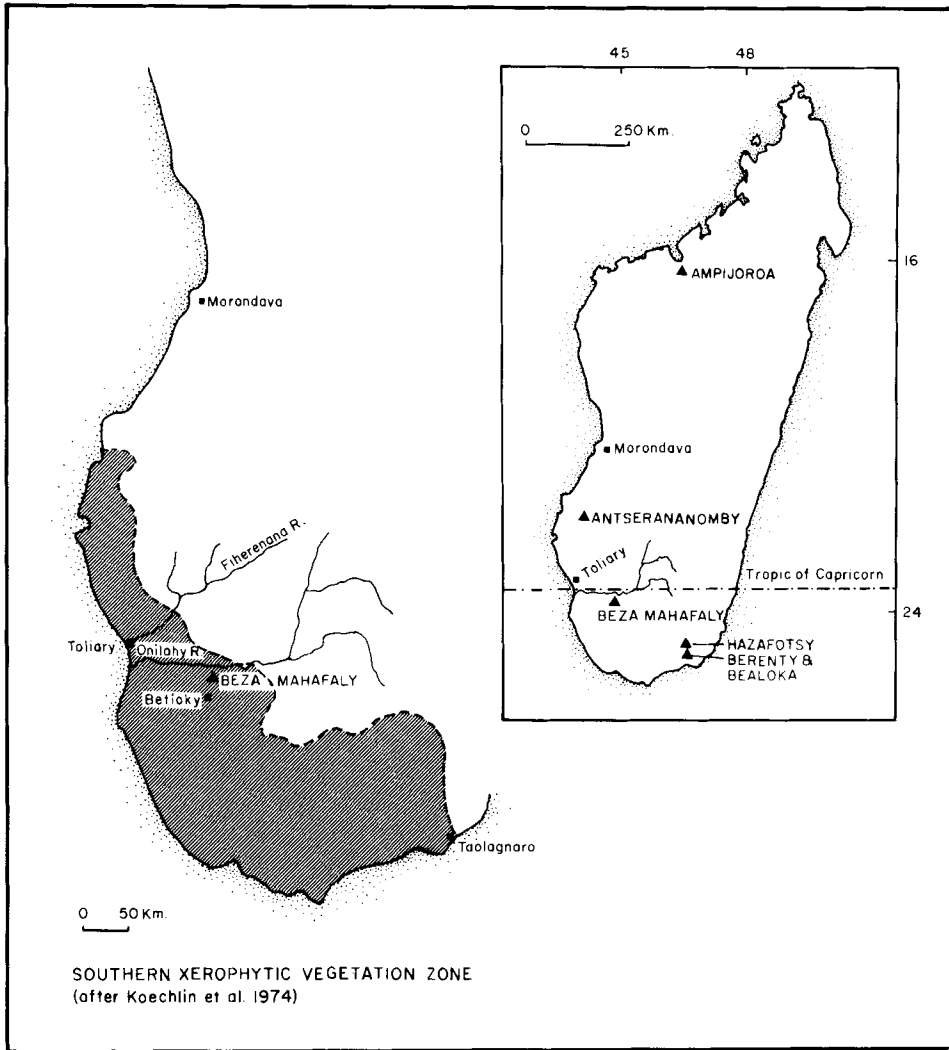
Fig. 1. Location of the Beza Mahafaly Special Reserve in southwest Madagascar.

at 100 m intervals. Additional information about group composition was gathered opportunistically throughout the study. When animals were located by sight or hearing away from the trail we tried to census them, because our goal was to count and, as far as possible, identify all animals. The presence of marked or naturally recognizable individuals in all groups minimized the likelihoood of inadvertently censusing the same group twice. While animals sometimes scattered to feed and rest during the day, all group members usually reunited by the end of the day or early next morning. During the annual census we tried to census all groups repeatedly, and only those counted at least twice were used in this analysis. When counts differed, the higher one was used. Because female dispersal is rare, we identified groups from year to year by their female membership.

The terms *transfer, visiting,* and *wandering* used in this paper require expla-

TABLE I. Changes in the Four Focal Groups: December 1984 to May 1985*

	Dec. 1984	Feb. 1985	Mar. 1985	May 1985
Sakamena Sud				
F #17 (adult)				
F #14 (1)				
M #4 (11)				
M #5 (7)		wanders	wanders	transfers
Vavy Goa				
F #54 (adult				
F #38 (adult)				
F #33 (2)				
M #11 (19)				
F #21 (juv)				
M #31 (6)				
M #26 (adult)				
Vavy Masiaka				
F #35 (adult)				
F #36 (17)				
F #37 (adult)	disappears			
M #25 (17)				
M #29 (6)	wanders	leaves		
M #30 (11)				
Vaovao				
F #19 (adult)				
F #20 (14)				
F #73 (18)	dies			
M #8 (14)	evicted	wanders	wanders	
M #7 (1)				
M #9 (juv)				
M #10 (9)		joins		
M #29 (6)		visits	joins	

*Estimated ages (in years or age classes) of animals in July 1985 are indicated in parentheses. F = female; M = male; juv = juvenile.

nation. Transfer implies a change of group membership. A male was said to have transferred if he consistently (i.e., for >1 month) rested, fed, and moved in proximity to a new group and slept near or in the same sleeping trees [Sauther, 1991]. The process of transfer sometimes (but not always) took several months and involved visiting and wandering. A male was said to be visiting if he divided his time between two groups. Some males, alone or in pairs, were seen on the periphery of several groups over a period of weeks or months, but were repeatedly chased away. Such males were said to be wandering. Not all visitors and wanderers transferred. Episodes of visiting and wandering that did not end in transfer may have been failed transfer attempts, or transfer may not have been the goal. Seasonal changes in transfer rates were not documented in this study because the population was not systematically monitored throughout the year. However, observations during 1984–85 suggest that transfers may be most common in the months preceding the mating season.

Disappearances of males 19 years or older were treated as deaths. Disappearances of males <19 years were treated as deaths only if they were not seen in another group in two successive censuses. This probably underestimates transfer rates, because it assumes that sifakas never disperse over long distances. However,

the high frequency of short-distance transfer within the reserve suggests that long-distance dispersal is rare [c.f. Sauther, 1991; Sussman, 1991, for male *Lemur catta*], and we have not found previously unaccounted-for collared animals in groups with home ranges that did not overlap those of the study population. We spent at least 1 day each year since 1986 surveying in progressively wider arcs around the reserve to a maximum distance of 1 km from the reserve boundaries. We encountered groups at a rate of 2.3/hr, but none contained unaccounted-for collared animals.

True rates of transfer may also be higher than the estimates presented here because our data come primarily from annual censuses and overlook periods of residence that occurred between censuses. Again, however, the 1984–85 data suggest that such short sojourns are uncommon.

Thirteen males in four social groups with adjacent home ranges were subjects of more intensive study in 1984–85 (Table I). Ten of these males were captured. Based on the small size of two males not captured, we identified them as natal males. A high degree of habituation was achieved within the first month of the focal study, and animals would approach and feed within 2–3 m of the observer (A.F.R.). Focal animal samples were collected together with ad libitium records of social interactions in the group or approaches to the group by other animals. Methods and types of behavioral data collected were similar to those in previous studies [e.g., Richard, 1978]. The scoring of agonistic episodes is considered here, however, because they figure centrally in the Behavioral Context of Transfer section.

Dominance relations between animals were determined according to the general critera developed by Sade [1967] and Hausfater [1975]. A decided agonistic interaction was one in which there was a clear loser, with one animal exhibiting only submissive signals while its opponent exhibited only aggressive behavior or no agonistic behavior. Following Jolly [1966: p. 60], Richard [1978: p. 131], Altmann [1980: p. 215] and Pereira et al. [1990], behaviors scored as aggressive were cuff, lunge, push, bite, and chase; those scored as submissive were chatter-call, retract lips, hunch back, and avoid. Animal X was said to have avoided Animal Y if Y approached to within 1 m of X and X glanced at Y and immediately moved at least 1 m away.

RESULTS
Size, Composition, and Persistence of Groups

Between 1985 and 1989, group size ranged from 2 to 13 individuals, with a preponderance of groups containing 4 to 8 members (Fig. 2). The mean socionomic sex ratio over the 5 years was 0.45 (expressed as the average fraction of females in the subadult and adult segment of a group), which was close to the mean sex ratio of 0.42 in the population as a whole [Richard et al., 1991]. This reflects the fact that all animals lived in bisexual groups and that even during transfer males were rarely outside groups for long. The pattern of variation in the fraction of females in groups differed significantly from a normal distribution, evidently because a disproportionately high number of groups contained fewer females than males (Fig. 3, Lilliefors maximum difference = 0.183, 2-tailed probability <0.001; data points are independent, i.e., only the first full census of each group was used). There was no systematic relationship between a group's sex ratio and its size: on average, 50–60% of the adults in a group were males, regardless of group size (Fig. 4).

Group histories are difficult to document conclusively within the sampling constraints of this study, because when a group was not seen during a census, we
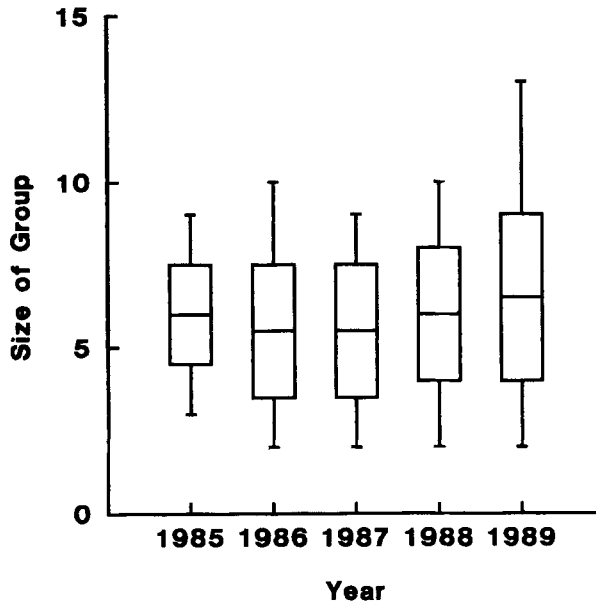
Fig. 2. Median group size and interquartule span and range of group sizes in the study population [n = 18 (1985); 21 (1986); 20 (1987); 17 (1988); 26 (1989)].

could not be sure whether it had been overlooked or had disintegrated. Conversely, a "new" group could just be a group that had been overlooked in previous censuses. The findings below are presented with this caveat in mind.

Twenty-one of the 27 groups identified in 1984–85 persisted until 1989. In 1989, these groups were composed of some or all the adult females originally identified and/or their female descendents, juveniles, and adult males. With rare exceptions, the male composition of all groups changed at least once between 1984 and 1989. From the annual censuses and patrols of the forest at other times, we infer that the home ranges of surviving groups changed little between 1984 and 1989. A group's home range usually overlapped with two or three others and, in one instance, with as many as five. The area of overlap with each neighbor was rarely more than 50 m wide, and most groups had exclusive use of a core area. Home ranges of the focal groups were estimated from sightings and from all-day follows during the focal study in 1984–85. Those of non-focal groups were estimated by connecting blocks in which sightings were made by the shortest pathway.

Six groups disappeared between 1984 and 1989. Four of the six consisted of an adult pair, or an adult pair with an immature offspring. The fifth contained two adult females and several males. All but one of the females in these groups were collared. None have been sighted outside their old home range, and we presume they are dead. Of the collared males in these groups, two were not seen again, one transferred to a neighboring group, and two paired with unmarked and unidentified females in new home ranges. The home ranges of these five defunct groups have been absorbed into those of neighboring groups. A sixth group, Fotaka (1985–86: two males, one female), apparently disintegrated and was then reestablished in the same home range with the same males. In 1987 we found only one of the males, but in 1988 both males were once again present in the Fotaka home range together
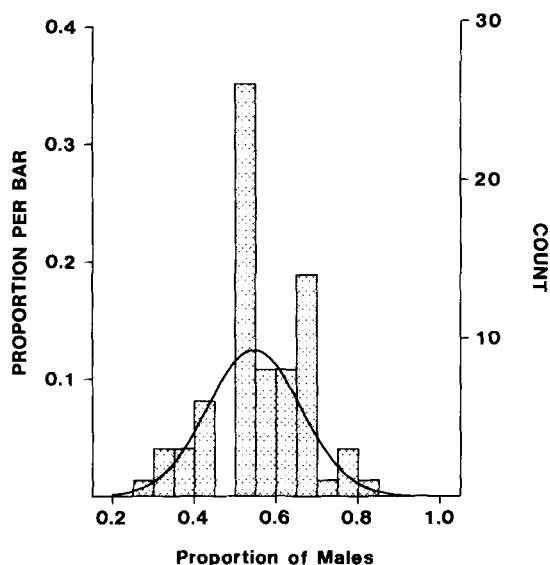
Fig. 3. Proportion of males in social groups in the study population, 1985–1989, with a normal curve overlaid. The scale on the right represents number of groups, and that on the left is standardized by the sample standard deviation [Wilkinson, 1988]. (N = 74 group censuses; not all points are independent, because they include censuses of the same groups in different years.)

with three new adult females. The group retained this composition in the 1989 census.

Six new groups were established between 1984 and 1989, each consisting of an adult male and female, occupying a small home range completely overlapped by neighboring groups (see below).

Patterns of Dispersal

Dispersal by female sifakas is rare, whereas all males leave their natal group. Upon leaving its group, a male could in principle do one of four things: live alone, live with other males, transfer into another group, or establish a new group with females. Some males disappeared during the study, and we do not know if this was due to dispersal out of the reserve, dispersal-related mortality, or mortality due to other causes. Most often, however, a male recorded as not present in his group of origin was subsequently found in a group nearby. Between 1984 and 1991, most males transferred at least once, and a few established new groups.

Rates of transfer. Transfer rates were highest among males aged 3–6 years, dropped precipitously in 7–8-year-olds, and fluctuated thereafter (Fig. 5). The high transfer rate among 3–6-year-old males suggests that, like most male primates, maturing male sifakas disperse from their natal group. In this study, all males of known birth year either died or left their natal group between the ages of 3 and 6 years (n = 17). The transfer rate was also high among 3–6-year-old males because they were more likely than older males to transfer two or three times (Fig. 6). One male (aged 3) captured in his presumed natal group (Fotaka) in 1985 was censused in another in 1986, a third in 1987, and in 1988 was found back in his natal home range with the newly reestablished group now occupying that range (see Size, Composition, and Persistence of Groups subsection above).

Distance of transfers. Most transferring males joined a neighboring group
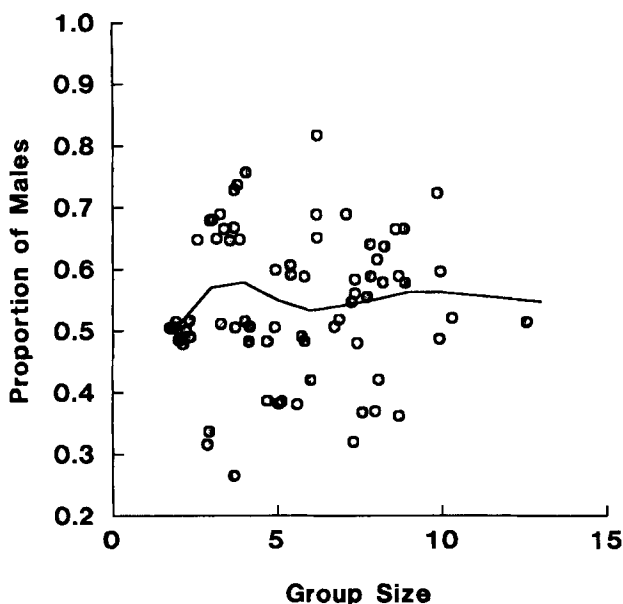
Fig. 4. Proportion of males in social groups of different size in the study population. The data are fit by LOWESS [locally weighted scatter plot smoothing; Cleveland, 1981]. To prevent symbols from overlapping, each point was plotted with a small amount of uniform random error. (N = 74 group censuses; not all points are independent, because they include censuses of the same groups in different years.)

with a home range overlapping their group of origin (Fig. 7A), and males did not move far from their group of origin, even after several transfers. Nineteen males, each censused for 5 consecutive years, moved in successive transfers no more than two home ranges away from their group of origin (Fig. 7B).

Composition of transfer groups. Ideally, this analysis should identify features of transfer groups distinguishing them from other potential transfer groups (i.e., all groups with home ranges overlapping a male's group of origin). We might expect males to target groups for transfer that have more or a higher proportion of females (to enhance their mating opportunities), and fewer males (to reduce intrasexual competition and the difficulty of gaining entry). Unfortunately, we do not yet have the data to undertake such an analysis. Instead, as a first step, we focus on 14 cases in which the composition of the group of origin and the group into which the male transferred were both reliably known at the time of transfer. Males of different ages showed different tendencies in their patterns of transfer [Fig. 8A: G (with William's correction) = 6.548, d.f. = 2, $P < 0.05$; Fig. 8B: G (with William's correction) = 6.041, d.f. = 2, $P < 0.05$]. The median age of males that moved to groups with a higher proportion and number of females was lower than that of males that moved to groups with the same proportion and number of females. Median age was highest among males that moved to groups with a lower proportion and number of females. [The number and proportion of females are not independent of one another (Kendall's tau = 0.579, $P < 0.01$).] Males transferred without regard to group size or the number of males present [for *Cebus olivaceus*, cf. Robinson, 1988].

Length of tenure. Fourteen males older than 6 years were censused annually for 5 or more years. Of these, only two are known to have remained in the same
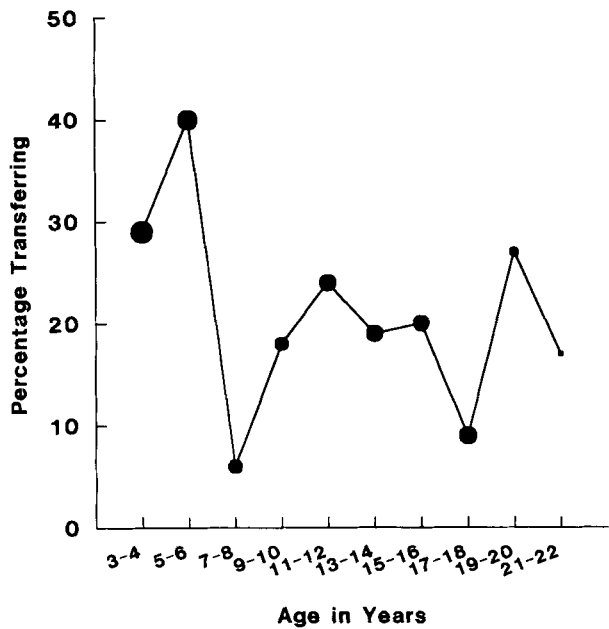
Fig. 5. Rates of transfer by males of different ages. Differences in sample sizes among age groups are indicated by differences in symbol size. (N = 191 cases in which males were observed for 2 or more consecutive years.)
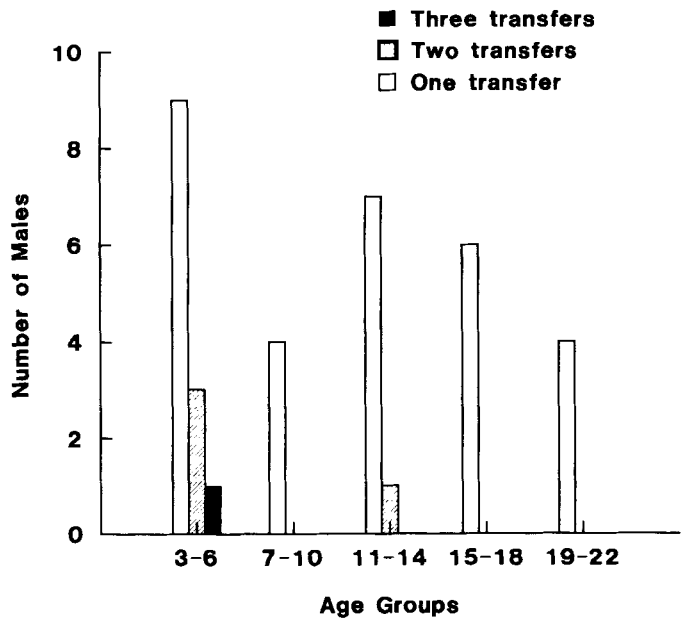

Fig. 6. Number of males in different age groups that transferred once, twice, or three times.

group for more than 5 years (6 and 7 years, respectively). One of them was the adult male from Fotaka Group, which disintegrated and reformed with new females in 1988.
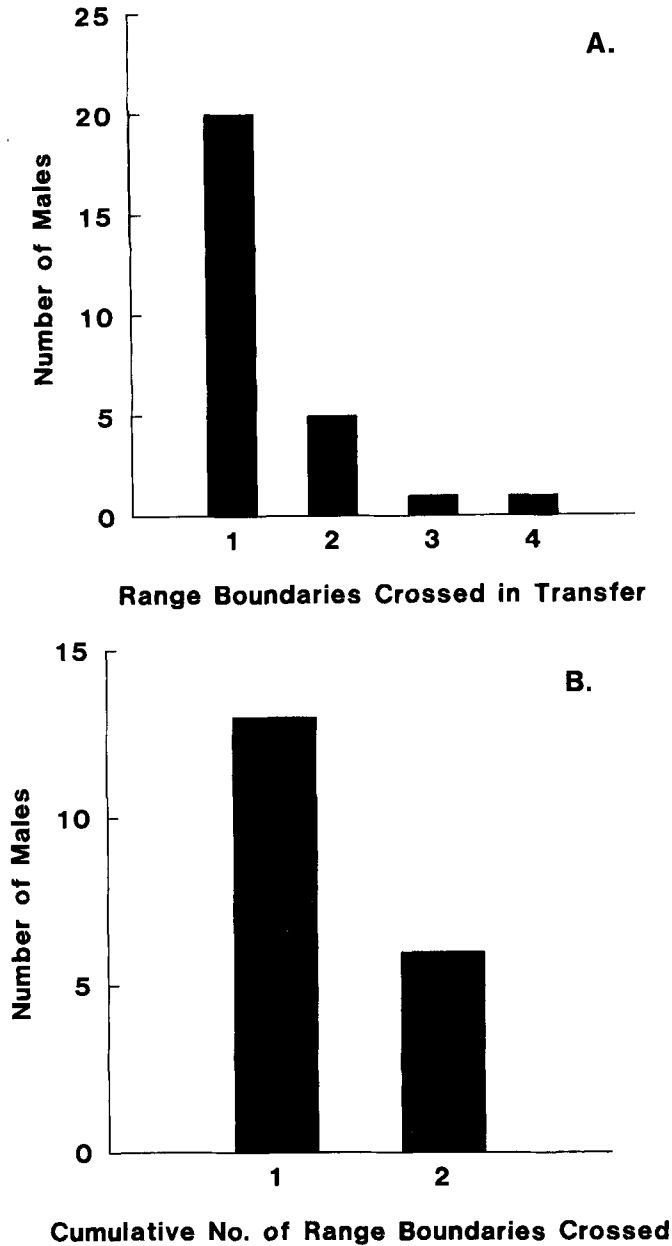
Fig. 7. **(A)** Number of home ranges away from group of origin moved by males in a single transfer (i.e., a male who moved to an adjacent group was scored as moving one home range away from his group of origin), and **(B)** number of home ranges away from group of origin moved by males, summing all transfers made by each male observed for 5 consecutive years.

Average tenure length is difficult to estimate because many males were present in the group when first observed and we do not know when they joined it, and others were still present in the group when last censused. The survival analysis technique [Kaplan & Meier, 1958] used to estimate tenure lengths among
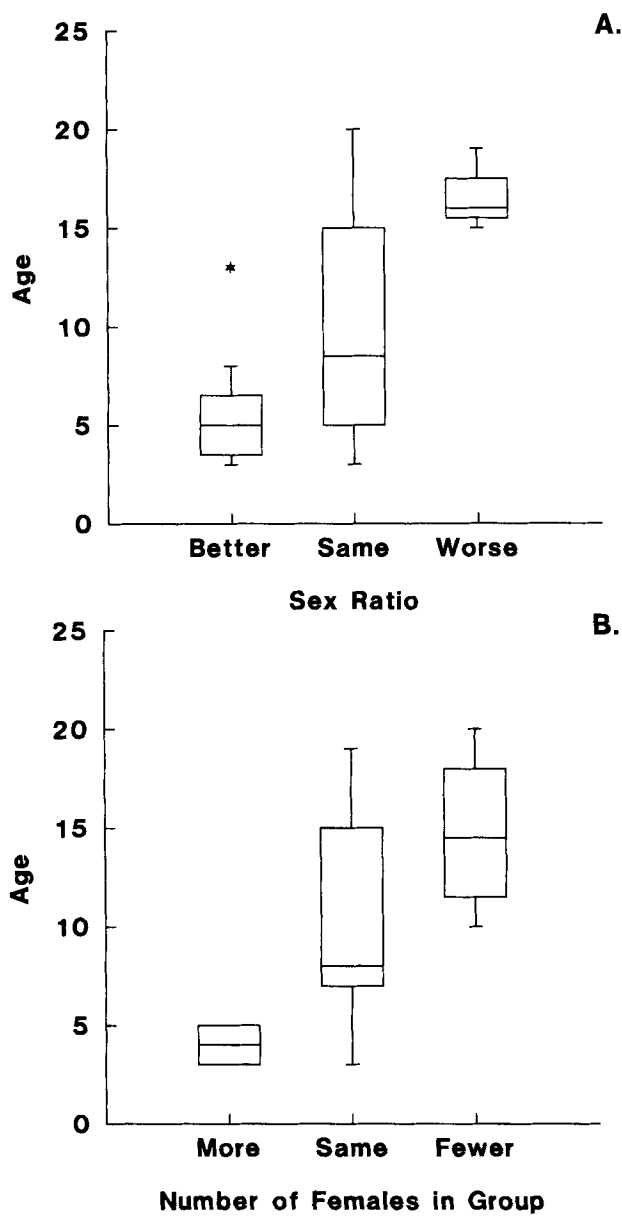
Fig. 8. Median and 25th and 75th percentiles (i.e., bottom and top of box), and range in the ages of males who transferred into groups in which (A) the proportion and (B) the number of females were higher than, the same as, or lower than in the group of origin (n = 14 males). Asterisk indicates an outlier.

males of different ages takes into account the latter (right-censoring) but not the former (left-censoring). By this analysis, median tenure length was about 3 years, and both the median and 25th and 75th percentiles were similar among males in age classes greater than 3–6 years (Fig. 9). Three to 5-year-old males exhibited shorter tenure lengths. These values underestimate the real tenure length of adult
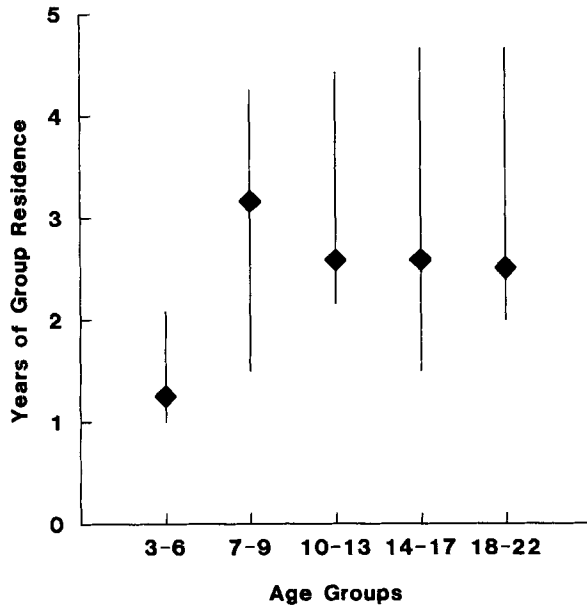
Fig. 9. Median and 25th and 75th percentiles for tenure length among males of different ages (Kaplan-Meier product limit estimation of survival). (N = 67 cases, including right- and left-censored cases.)

males by an unknown factor, because of censored observations. However, given the high rates at which males are known to transfer, we consider it unlikely that the real values are substantially higher.

Female dispersal. Female dispersal was rare. Six females in this study evidently left their groups of origin to establish new groups (see below). There was one possible case of transfer. A young female disappeared from a focal group during the mating season in 1985 and was presumed dead. In 1989, a new adult female appeared in that group. Based on natural markings, we identified her as the female who disappeared in 1985. She was captured in 1989, with an estimated age at that time of 9 years. Much hinges on our identification: if the group she joined in 1989 was *not* her natal group, this would constitute a unique instance of transfer by a female into a group of unrelated females. The formation of social relationships between non-matrilineally related females was not implicated in the only other case of female movement: two neighboring females (aged 17 and 12 years, respectively) switched home ranges and males (aged 17 and 15 years) between 1986 and 1987.

Founding new groups. Males and females formed new groups together in six cases. Each of these groups comprised an adult pair living in a small, interstitial home range overlapped completely by the larger groups around it. The males in these groups were 12–19 years old. We know something of the dispersal history of five of them. Two became part of new groups when the (marked) female(s) disappeared in the groups to which they previously belonged. We presume these females died. Three males had a history of wandering prior to establishing new groups.

Two of the females that formed new groups had been captured. Both were less than 6 years old at the time of dispersal and nulliparous. The context of departure of these females from their natal groups is not known.

Behavioral Context of Transfer

The behavioral context of transfer provides insights into the proximate mechanisms underlying transfer patterns, and we now consider briefly the circumstances under which males left, joined, or tried to join the four focal groups between November 1984 and May 1985.

During 250 hr spent observing 13 males in the four focal groups, Sakamena Sud, Vavy Goa, Vavy Masiaka, and Vaovao, there were six episodes of departure, entry, and attempted entry by males (Table I). One male transferred between two focal groups, but otherwise only departure or arrival was witnessed. Several behavioral patterns were associated with transfer. One male [#5 (7 years)] seemed to drift out of his group. A second male [#29 (6 years)] was subject to some aggression from other group members, though not targeted aggression or eviction [Vick & Pereira, 1989; Richard & Heimbuch, 1975]. A third male [#8 (14 years)] was probably evicted from his group, and he was certainly the only male seen being chased away by a female. In other episodes, resident males did the chasing. For males #5 and #29, entry to a new group was a gradual process that began with visiting. These episodes are described in more detail below.

Departure. In December 1985, male #5 (7 years) was regularly seen with Sakamena Sud members. He and the other male in the group, #4 (11 years), each initiated aggression against the other, but interactions between them were rare and in fact they spent little time in proximity to one another. Their relationships with the females of the group, a mother and her presumed 18-month-old daughter, were not much more informative. Each was once seen submitting to one of these females, and each engaged in occasional grooming bouts with the females. Male #4 spent more time than #5 close to the females, particularly the mother. Male #5 moved in and out of the group during February 1985. He was sometimes sighted alone, and twice he was seen being chased away by members of an unmarked neighboring group (Fotsy). By May 1985 he was visiting Fotsy without conflict while still maintaining ties to Sakamena Sud: for instance, he participated with other Sakamena Sud members in a chase of Vaovao. He was censused in Fotsy in 1986, and has not been seen in Sakamena Sud since then.

Male #4 belonged to Sakamena Sud from November 1984 to June 1988. Since August 1989 he has been found alone outside the group's home range.

Vaovao contained two small males and only one clearly adult male, #8 (14 years), in early December 1984; male #8 was the subject of aggression by female #20 (14 years) in two of the four agonistic episodes seen that month. When observations were resumed in early February, #8 was no longer in the group. Over the next few days he was sighted alone, within or on the edge of Vaovao's home range, or on the periphery of the group itself. Animals in the group mostly appeared indifferent to his presence, though once female #19 (adult) approached him and he groomed her briefly until she moved away. He also rested briefly with male #7 (1 year), until male #10 (9 years) and female #20 chased him away. When male #8 tried to approach the group again later, #10 chased him away. We subsequently saw him alone within the home range of Vavy Goa, being chased out of Sakamena Sud's home range by #4, and being chased out of Vavy Masiaka's home range by the three males in that group. He was seen in another group in the 1986 census, but has not been sighted since then.

Approach or entry. Male #10 (9 years) joined Vaovao between December 19th and February 5th; this was also when #8 (14 years) left the group. In February, we saw #10 initiate aggression against the two juvenile males and against male #29 (6 years) when he visited. These three all exhibited submissive behavior

to male #10. Only male #29 was observed mating in that group in March [Richard, 1992].

Male #2 (11 years) approached Vavy Goa once, in May 1985. For 10 min he was chased by, and counterchased, two of the young adult males in the group, and then #2 moved off. Other animals in the group did not appear to pay much attention.

Transfer. In December 1984, male #29 (6 years) was the youngest of three males in Vavy Masiaka, and he was strongly affiliated to one of the two adult females in the group. He looked and behaved like a natal male. He was the most frequent target of aggression and displacements in the group, gave submissive signals to both adult females, and was consistently displaced by the other two males.

In February 1985, #29 moved back and forth between Vavy Masiaka and Vaovao. Although subordinate in both groups, he visited without conflict and seemed readily accepted in both. He was present but did not participate when male #10 (9 years) chased #8 (14 years) away from Vaovao early in the month; later, back in Vavy Masiaka, he joined the other two Vavy Masiaka males in chasing male #8 away from that group. In late February, he returned to Vaovao and mated repeatedly with female #20 (14 years), with little opposition from other males present. After this, he stayed in Vaovao and was dominant to other males in the group. In June 1986, he visited Sakamena Sud, but thereafter was sighted only in Vaovao.

DISCUSSION

For a male sifaka about to leave his group at Beza Mahafaly, the social landscape consisted of an array of groups of different sizes and changing individual membership, three to five of which he was likely to encounter regularly on the edges of the home range of his own group. Socionomic sex ratios varied widely, but at any one time more than a third of the groups in the reserve were likely to contain equal numbers of males and females. Major changes in this landscape occurred in two ways: through the disintegration of existing groups and the formation of new ones.

Males moved between groups quite frequently, with most moves taking place over short distances. Age differences among males and differences in their previous history contributed to differing patterns of movement. All males left their natal groups and transferred into neighboring or nearby groups. Three to 6-year-old males were more likely than older males to transfer more than once, and to join groups with a higher proportion and number of adult females. Older males transferred too, but they did so at a lower rate and were progressively more likely to join groups with a lower proportion and number of females. Dispersal by males aged 3–6 years appeared to be voluntary, whereas dispersal by older males occurred through eviction. Males and females sometimes paired up and established new groups. Where known, the females of these pairs were young and nulliparous, whereas the males were older and their previous mates had died, or they had not been successful in joining an existing group. Only two adult males are known to have remained more than 5 years in a single group.

The female composition of groups helped determine their attractiveness to young transferring males, whereas neither group size nor the number of males present appeared important. While younger males evidently targeted groups with a higher proportion and number of females than their group of origin, the presence of potential mates was not the only factor determining which group a male would join: the behavior of resident males toward a newcomer was certainly an important

determinant of whether a male gained entry. This behavior was quite variable. It was perhaps conditioned by previous knowledge of the approaching male, and by variation in the vigor or number of resident males present. Older males were more likely to transfer into groups with a lower number and proportion of females, a finding that demands separate explanation. Possibly, older males only gained entry to groups containing younger male relatives who tolerated their presence. Most likely, the mechanisms and outcomes of dispersal by older males are complexly determined by their age, condition, kinship network, and previous history in the neighborhood.

Among social mammals, male dispersal is characteristic of species in which the average age of females at first conception is greater than the average length of residence of breeding males, whereas female dispersal occurs in species in which these temporal relations are reversed [Clutton-Brock, 1989]. In the Beza Mahafaly population, females bred for the first time when they were 5 years old. Only two adult males remained in the same group for more than 5 years in this study, and the longest tenure recorded so far is 7 years. Our limited results are consonant with Clutton-Brock's [1989] findings, although real tenure lengths are probably somewhat longer than those estimated in this analysis. Indeed, we predict that 6–8 year tenures will become more common in our data set as the study continues: if maturing daughters and their mothers eject the male that sired those daughters, tenure should be longer when mothers first give birth to sons or to daughters that die as infants or juveniles. The observation that females helped evict males but did not prevent new males from entering the group, provides further support for the idea that increasing likelihood of consanguinity precipitates the ejection by females of older males from groups in which they have long been resident. Additional data on completed tenures and the relationship between the sex of offspring and tenure length are needed to examine this hypothesis further.

Six dispersing males paired up with females and established new groups. Three had a history of wandering and failure to gain entry to existing groups. It is unclear why females left their natal groups with such males. However, we know that two were nulliparous and less than 6 years old. One explanation for their departure is that the onset of reproduction is delayed in young females in groups with several reproductively active adult females, and dispersal may enable them to begin their reproductive careers. Socially mediated delays in the onset of reproduction are reported in many mammals, including some primates [Abbott, 1984; Epple & Katz, 1984; Goldizen, 1987; McClintock, 1983]. Indirect support for some mechanism of reproductive suppression in sifakas is provided by the observation that no more than two infants in a single group in one birth season have been reported for any sifaka population, regardless of the number of females present of reproductive age [Richard et al., 1991]. Adult females may precipitate dispersal by targeting young females for aggression and eventual expulsion from the social group. This has been reported among semi-free-ranging *Lemur* spp. [Vick & Pereira, 1989].

This study supports the general proposition that sifaka social relations transcend the boundaries of social groups. Indeed, links of familiarity and relatedness between animals in different social groups are probably more common among primates and other vertebrates than once realized [e.g., Cheney, 1987; Rowell, 1988], and are simply easier to detect and study in species like lemurs that live in groups with small, overlapping home ranges. However, the pattern of transfer by sifaka males between neighboring groups and the variable behavior associated with transfer strongly suggest that analyses of the sifaka social and reproductive system should recognize the importance of the social group itself as well as the

larger unit of the neighborhood. Future analyses require more extensive data on lifetime patterns of transfer and mating by males. For example, do transferring males really target the group with the most favorable sex ratio or greatest number of females from among an array of variably composed groups around their group of origin? Does long-distance dispersal occur in the absence of good local options? We know that sifaka society is not as viscous as the results of this study imply: reports of sifakas in small, isolated forest fragments indicate that long-distance dispersal does occur, but the conditions favoring it are unknown.

For 3–6-year-old males, transfer involves little aggression from members of their group of origin or members of the transfer group. Departure seems to be voluntary, and the process of joining a new group gradual and uncontested. The lack of aggression by adult resident males toward these young newcomers may signal that they are sexually immature and seeking future, not present, opportunities to mate [i.e., a "hamadryas" style strategy; Abegglen, 1984]. The youngest male observed mating or attempting to mate was 6 years old. In contrast, secondary transfer occurs when resident adult males are driven out of the group by females and males in concert; we infer that female group members thereby expel close consanguineal male relatives, while males simply seize the opportunity to reduce the field of competition. Intrasexual competition may subsequently prevent these expelled adult males from joining another group.

Genetic information as well as further behavioral data will be needed to go beyond speculative inferences about the relative importance of intrasexual competition and inbreeding avoidance in determining dispersal in the Beza sifaka population. In this paper, we have assumed that female group members are closely related to one another, and that the males transferring into a group are unrelated or only distantly related to its females. The first of these assumptions is well supported empirically. However, most primates transfer to neighboring groups [Pusey & Packer, 1987], and sifaka males are no exception. Short-distance dispersal, plus the frequency with which sifaka males evidently mate outside their own group, call into question the idea of a genetic dichotomy between natal and non-natal males. This, in turn, undermines the rationale for the hypothesis that male dispersal is driven by inbreeding avoidance on the part of females [cf. Pereira & Weiss, 1991]. A more narrowly focused avoidance of *extreme* inbreeding, or incest [i.e., matings between father and daughter, mother and son, or siblings; Shields, 1987, 1988], may be more important in sifakas than avoidance of mating with more distantly related kin.

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