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BALANCING COSTS AND OPPORTUNITIES: DISPERSAL IN MALE BABOONS

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Abstract.—Young male baboons typically disperse from their group of birth as they near adult size and may continue to migrate between social groups throughout their lives. Long-term data on dispersal and residence patterns of male baboons in Amboseli National Park, Kenya, were available for 110 males in the population, including 43 that were monitored during their natal dispersal. These data enabled us to provide not only a detailed evaluation of the effects of reproductive competition on dispersal but also the first direct estimates of the costs of dispersal in male primates and one of the few direct estimates of fitness costs associated with breeding in the natal group. Males underwent natal dispersal at a median age of 8.5 yr (range, 6.8–13.4 yr) and subsequently remained in nonnatal groups for a median tenure of 24 mo (range, 1–138 mo). Half of the males in the study engaged in moderate to extensive reproductive activity before natal dispersal. Reproductive costs associated with breeding in the natal group were suggested by the high mortality of offspring for whom natal males were their likely fathers, even though maternal relatives avoided mating with each other. Dispersal involved considerable time spent alone, and therefore the costs of dispersal were substantial, because of mortality risks and missed reproductive opportunities during dispersal. Female availability and male mating success apparently affected both natal and secondary dispersal patterns. We present a model of dispersal tendency in order to explicate the ways in which differences in population density, predation risk, and the distribution of mating opportunities among groups might result in complex dispersal patterns that are consistent with both the results of the present study and the disparate empirical reports in the literature.

Dispersal of offspring or propagules is a universal trait of living organisms, although the frequency of dispersal and the distance traveled during dispersal vary widely. This variation has motivated a number of theories about the adaptive significance of dispersal, the costs and benefits of dispersal versus philopatry, and the population genetic consequences of dispersal patterns (see, e.g., Wright 1931, 1943, 1965; Gadgil 1971; Hamilton and May 1977; Shields 1983; Johnson and Gaines 1990). In addition, because most terrestrial vertebrates exhibit a sex bias in dispersal, a number of theories have been developed to explain cases in which one sex disperses with greater frequency or over greater distances than the other (see reviews in Greenwood 1980; Dobson 1982; Moore and Ali 1984; Shields 1987; Johnson and Gaines 1990).

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Among primates, male dispersal is the most common pattern. Of 21 well-studied species, 16 exhibit predominantly or exclusively male dispersal (Pusey and Packer 1987a). This pattern in which males disperse and females are philopatric (or, more appropriately, *matrilocal*, the term used in anthropology) may be related to the fact that females in many primate societies acquire disproportionate competitive advantages when they remain with relatives (Harcourt et al. 1976; Wrangham 1980; Andelman 1986) or that familiarity with the home range may be more important for females than for males (Waser and Jones 1983; Pusey and Packer 1987a). Combined selection pressures, for inbreeding avoidance and for females to remain with relatives or in the natal home range, may result in the evolution of male-biased dispersal (Packer 1979a; Pusey 1987; Pusey and Packer 1987a). Alternatively, or in addition, sex differences in competitive intensity may select for male-biased dispersal. Although departure from the natal group is typically not accompanied by aggression among primates that live in multimale, multi-female groups (Pusey and Packer 1987a), males may both avoid competition with male relatives and encounter greater numbers of potential mates by dispersing (see discussions in Moore and Ali 1980; Dobson 1982; Waser 1985; Pusey 1987). For females, leaving relatives and encountering more potential mates may not represent advantages, with the result that selection pressure to disperse is stronger on males than on females.

The effects of intrasexual competition on dispersal have been difficult to establish in primates, although evidence suggests that males in a number of primate species disperse in response to female availability (e.g., baboons: Packer 1979a; Manzollillo 1986; blue monkeys: Henzi and Lawes 1987; sifakas: Richard et al. 1992; lemurs: Sussman 1992). Evidence in support of the inbreeding hypothesis is more abundant but largely indirect (Pusey 1987). Direct evidence comes from one wild baboon population in which an estimated 40% reduction in offspring viability occurred for a single male that bred in his natal group (Packer 1979a) and from several captive primate populations (Ralls and Ballou 1982), humans (Cavalli-Sforza and Bodmer 1971), and wild populations of nonprimate vertebrates (Greenwood et al. 1978; Pusey and Packer 1987b; Keane 1990). However, in some vertebrate populations, breeding in the natal group apparently does not impose a fitness cost (see, e.g., Rood 1987; Bulger and Hamilton 1988).

Whether dispersal in primates has evolved as a result of inbreeding risks or competition, mortality risks and opportunity costs associated with movement between groups have probably also played a role in shaping dispersal patterns. Indirect evidence from several species (reviewed in Dunbar 1987; see also Isbell et al. 1993) suggests that dispersing animals may be more vulnerable to predation and other causes of mortality than those that do not disperse. Further, if dispersing animals spend time living alone, they experience opportunity costs during dispersal by losing chances to mate (mating by extragroup or solitary males is common in some species of primates but is atypical for baboons; see, e.g., Cords 1987; Sprague 1992). This opportunity cost has not previously been addressed in any detail.

The importance of dispersal in the lives of male baboons cannot be overestimated. If dispersal increases the risk of mortality, it will affect the likelihood of survival to adulthood for males that emigrate as juveniles or subadults and will

affect the reproductive life span of males that disperse repeatedly during their lives. Because male baboons are more likely to transfer into groups with high numbers of cycling females (Packer 1979a; Manzollilo 1986), dispersal may also affect mating success. Dispersal therefore influences every component of lifetime reproductive success, and variability in dispersal patterns may be a crucial source of variance in fitness for male baboons.

Although the importance of dispersal has long been recognized, little empirical evidence has been available to evaluate costs of dispersal, costs of remaining in the natal group, and effects of competition on dispersal. In this study we present results of an analysis of dispersal patterns in a well-studied population of wild baboons. Our work includes the first direct estimates of the costs of dispersal in male primates, one of the few direct estimates of fitness costs associated with breeding in the natal group, and the most complete analysis to date of the effects of reproductive competition on dispersal. In addition, we examine the effects of male age and associated factors on dispersal. Finally, we explore the premise (see, e.g., Bengtsson 1978; Packer 1979a; Shields 1987; Johnson and Gaines 1990) that the observed dispersal patterns are determined by a balance between these reproductive costs and opportunities.

METHODS

Study Population and Data Collection

The subjects of the study were male baboons (*Papio cynocephalus*) living in and around Amboseli National Park in southern Kenya. The baboon population in the Amboseli basin has been the subject of ongoing studies for two decades (see, e.g., Altmann 1980; Hausfater et al. 1982; Altmann et al. 1988; Altmann 1991; Muruthi et al. 1991). This population has been relatively stable in size over the 20-yr period of this study, although it experienced appreciable decline during the previous decade (Altmann et al. 1985). Dispersal events in three main study groups have been recorded on a routine basis as part of daily censusing since 1971 for Alto's group, 1977 for Hook's group, and 1984 for Lodge's group. Six other groups in the basin have been censused regularly since 1981, and most emigrations and immigrations involving these nonstudy groups have been recorded to within 1–2 mo of occurrence.

Age at natal dispersal (dispersal from the group of birth) was calculated for a sample of 43 males, born into Alto's and Hook's groups, that survived to at least 6 yr of age. Histories of secondary dispersal (dispersal from subsequent, nonnatal groups) were evaluated for 87 males (including 20 of the 43 natal males) in eight social groups and were used to calculate lengths of residence in nonnatal groups. In addition, 27 males, one-quarter of the sample, were known to have lived as solitary males; that is, they were seen alone at least once (and usually repeatedly) after emigration. Information on time spent alone has been recorded throughout the study.

Parameter Estimates

Overview.—Our aim was to identify both the causes of dispersal and the consequences of different dispersal and residence patterns. In order to estimate the

fitness consequences of dispersal and of remaining in the natal group, we needed direct mortality estimates for males and their offspring under varying conditions. In addition, we needed estimates of the opportunity costs that males incurred as a result of living alone during dispersal. To investigate the predictors of dispersal, we used measures of female availability, male mating success, and male age, as well as descriptions of family characteristics for maturing males. Preliminary analyses indicated that neither rainfall patterns nor seasonality predicted timing of dispersal; therefore, these effects were not considered further as covariates of dispersal. The various sorts of data used in these analyses and the methods employed to evaluate them are described in detail below.

The cost of reproducing in the natal group.—We examined the proposition that natal males experienced inbreeding depression when they mated in the natal group by comparing mortality for estimated offspring of natal and nonnatal males. Paternity estimates were made on the basis of long-term records of female reproductive state and mating behavior in Alto's and Hook's groups. While genetic data are preferable over behavioral data as a means of assigning paternity, such data are unlikely to become available for fetal losses or early neonatal deaths in wild populations; behavioral data will always be required to assign paternity to nonsurviving fetuses and infants, as we have done here. Although the correlation between mating success and paternity awaits genetic confirmation in this population, we feel there are several justifications for using these behavioral paternity assignments in the current analysis.

First, while some studies, particularly of captive populations, have shown poor correlations between behaviorally assigned mating success and genetically determined paternity (see, e.g., Curie-Cohen et al. 1983; Stern and Smith 1984); among Amboseli baboons, the correlation is likely to be good: because of the high visibility in the environment and the fact that relatively few females are in estrus on any given day (usually zero to two), virtually all copulations that occur while observers are with the group are recorded. Copulations that took place at night or during days when observers were not with the group may have resulted in conceptions. However, in Amboseli most copulations occur during periods of close mate guarding called consortships (Noë and Sluiter 1990; J. Altmann, unpublished data; see below), which often persist over several days and nights. Thus, even for those conceptions that occurred when observers were not with the group, the number of potential fathers is probably limited to the few males (two, on the average) that were seen consorting with the female during the conception period (see also discussion in Bercovitch 1992). The fact that we apportioned paternity assignments among all such males that shared likely conceptions (see below) reduced the chance of relevant error in our estimates, as did the fact that our estimate involved no bias in the assignment of paternity to natal or nonnatal males.

Female reproductive state was evaluated on a near-daily basis throughout the study period by visual examination of the sexual skin, which swells during the follicular phase and shrinks during the luteal phase of each 32-d cycle. These detailed records were used to pinpoint the days of most likely conception for each conceptive cycle (see Hendrickx and Kramer 1969; Wildt et al. 1977; Shaikh

et al. 1982). During the days of the late follicular phase of the sexual cycle, females engage in sexual consortships, periods of close, persistent following and sexual behavior between an adult male and an adult female (Hausfater 1975; Packer 1979*b*; Smuts 1985; Bercovitch 1987; Noë and Sluiter 1990). Virtually all mating takes place in the context of these consortships, which are typically quite conspicuous. Female characteristics such as agonistic dominance rank and age do not affect the probability that a mature female will consort or conceive, nor is there assortative mating by dominance rank among males and females (Packer 1979*b*; Rasmussen 1983; Altmann et al. 1988). All instances of sexual consortships between cycling females and adult males were recorded when observers were with the group. Baboons do not reproduce seasonally, and females cycle relatively asynchronously. The relatively small number of females cycling at any given time, combined with the conspicuous nature of baboon mating behavior, meant that mating activity could be monitored reliably and easily throughout the study.

By examining records of consortships and copulations for each conceptive cycle (see also Altmann et al. 1988) we assigned likely paternity to 164 pregnancies in Hook's and Alto's groups between January 1980 and December 1988, the period during which observers were with the groups almost daily and paternity assignments consequently could be made with the greatest confidence. We counted the number of conceptions for which only natal males or only nonnatal males were likely fathers and examined the fates of these conceptions. Because the paracallosal skin turns pink soon after conception and remains pink until the female gives birth or miscarries (Altmann 1970), we were able to include both pre- and postnatal mortality in calculating infant mortality. An infant was counted as having died if it survived less than 30 d after birth, for comparability to Packer (1979*a*) and Bulger and Hamilton (1988) and because these early deaths were more likely to have congenital causes than were later deaths. Results did not change if we extended the period to 90 d after birth.

We also investigated the extent to which males living in their natal groups avoided mating with, or were avoided as mating partners by, maternal relatives. For each male that actively consorted in his natal group, we compared his consort time with relatives and with nonrelatives, as follows. Following Packer (1979*a*), we counted the number of days that females were consorted (female consort days) while each young male was mature and in his natal group. For each natal male, we then compared the proportion of available female consort days that he attained with nonrelatives with the proportion of female consort days that he attained with female relatives. For example, if a male attained 15% of the available female consort days of nonrelatives, he should also have attained 15% of the consort days of his relatives if baboons do not avoid relatives. We compared the two values using a Wilcoxon signed-ranks test to determine whether adult males mated with female relatives a significantly lower proportion of the time than they mated with nonrelatives.

The costs of dispersal.—The difference in mortality rates for group-living versus dispersing males represents the mortality cost of dispersal. However, male mortality rates in species with male dispersal are difficult to estimate because an appreciable proportion of males disappear, which makes it difficult to distinguish

between death and dispersal (see also Waser et al. 1994). The data set used here includes 65 known emigrations, 20 likely emigrations, 20 known deaths, and 35 unexplained disappearances from Alto's and Hook's groups. A known emigration was counted whenever a male that disappeared from one group subsequently appeared in another or was seen alone. A likely emigration was counted in three circumstances: if the male had a recent history of leaving and entering the same group and then disappeared without returning ($N = 2$); if a prime natal male disappeared without indication of predation or illness, particularly if his disappearance followed recent periods on the periphery of the group or alone ($N = 14$); and if a male that experienced poor rank attainment, frequent harassment by resident males, and low mating success disappeared within 1 yr after he immigrated ($N = 4$; we included these four males as likely emigrations based on known fates of other males with similar histories). A disappearance was counted as unexplained whenever males disappeared in circumstances not included above. In these cases, exhaustive searches were usually conducted to determine whether these males were living alone or had immigrated into neighboring groups without detection. In a number of cases we located males that had disappeared, sometimes months later, living in new groups or as solitary males. For each male that was seen alone, careful searching was conducted on a regular basis to monitor his movement patterns and fate. Using these data we estimated male mortality rates in two ways each for dispersing and for group-living males, in order to provide a reasonable range of estimates for the mortality costs of dispersal in this population.

Mortality among dispersing males.—Mortality risk associated with actual entry into a new group is very low: fatal wounding by conspecifics is rare and has never been associated with immigration in this population. Instead, in baboons, most of the mortality that occurs during dispersal probably results from predation during the time spent alone between emigration and immigration, which ranges from a few hours to over a year in this population. Therefore, mortality among solitary males is probably a good measure of the mortality associated with dispersal. For our first estimate of the mortality rate of dispersing males, M_d , we counted the number of known and suspected deaths among solitary males and divided this count by the total number of male-months during which all males lived alone. We counted disappearances of solitary males as suspected deaths whenever extensive searching after the last sighting yielded no information about whether these males had immigrated into social groups or were still living alone. Two potential biases exist in this estimate of mortality during dispersal, each working in a direction opposite to the other. Some of the lone males that disappeared may have joined groups outside of the basin, which would lead to an overestimate of the number of deaths among these solitary males. However, the solitary males for which we had the most information on time spent alone were typically those males that stayed in or near the home range of their most recent group. This subset of dispersing males probably reduced their mortality risk by staying in familiar areas (Isbell et al. 1990); if they are overrepresented in our sample, our estimate would be an underestimate of mortality for solitary males in general.

For our second, alternative, estimate of the mortality rate of dispersing males, M_d , we compared the numbers of immigrants into Hook's and Alto's groups with the number of known and likely emigrants from these groups over the entire study period. Assuming that the population is neither a source nor a sink for dispersing males and that the number of solitary males was the same at the beginning and end of the study period (a reasonable set of assumptions for Amboseli; see Samuels and Altmann 1991), the proportion of males that died during dispersal was $1 - (I_T/E_T)$, where I_T is the total number of immigrants over the study period, and E_T is the total number of emigrants (Waser et al. 1994). Because an appreciable proportion of males disappear in circumstances that make it difficult to distinguish between death and dispersal, E_T was calculated as the number of known and likely emigrations plus a proportion of the unexplained disappearances. We assumed that unexplained disappearances, D , consisted of emigrations and deaths in the same proportions as did disappearances of known fate. That is, we assumed that emigrations among unexplained disappearances occurred in the proportion $E/(X + E)$, where E represents the number of known and likely emigrants, and X represents the number of known deaths. This gives

$$E_T = E + D[E/(X + E)] .$$

A mortality rate was estimated from the proportion I_T/E_T by using the median number of months spent alone by solitary males in the sample as the time period over which to distribute mortality. That is, if m is the median number of months spent alone, then $I_T/E_T =$ survival over m months, and ${}^m\sqrt{(I_T/E_T)} =$ survival over 1 mo, or monthly survival. Therefore, $1 - {}^m\sqrt{(I_T/E_T)}$ represents monthly mortality for dispersing males, M_d .

Mortality among group-living males.—First, we obtained an estimate of the mortality rate for group-living males, M_g , by considering the number of known deaths, the number of known and likely emigrations, and the number of unexplained disappearances in the population. As in our calculation of mortality among dispersing males, we assumed that deaths among unexplained disappearances occurred in the same proportion as deaths among disappearances of known fate, $X/(X + E)$, where E represents the number of known emigrants (known because they were seen alive after leaving the group) and X represents the number of known deaths monthly. This gives

$$X_{\text{est}} = (D)[X/(X + E)] ,$$

where X_{est} is the number of estimated deaths among the unexplained disappearances, and

$$M_g = (X + X_{\text{est}})/N ,$$

where N is the number of males in the group at the start of any given month.

A second estimate for the mortality rate of group-living males was obtained by examining deaths in this population that had known causes. All such deaths were caused by illness, conspecific wounding, or predation. Deaths caused by illness or conspecific wounding were unlikely to go undetected because the afflicted

animal rarely died instantly. Therefore, deaths of females for which causes could not be assigned were likely to be deaths by predation. Similarly, essentially all unexplained disappearances of males were almost certainly either deaths by predation or attempted emigrations. Based on the small sample of deaths with known causes in this population (17 for adult females, 15 for adult males), monthly predation risk was 13% lower for adult males than for adult females in groups. Therefore, we obtained a male mortality estimate by inferring that mortality for group-living males is roughly 13% lower than mortality of females.

The opportunity cost of dispersal.—Finally, we used the amount of time spent alone by dispersing males as an indicator of the reproductive opportunity cost of dispersal. Although the magnitude of these costs is surely highly contingent, we assume that in any given set of conditions the cost will be a nondecreasing function of the time spent alone, and we offer our data as evidence that such opportunity costs may be appreciable.

Female availability.—As an index of the number of “excess” males in the group, we used the number of adult males minus the number of cycling females in each month and examined the relationship of this measure to male emigration and immigration rates. Monthly data for numbers of males, cycling females, emigrations, and immigrations were examined for a period totaling 175 group-months in Alto’s and Hook’s groups.

Male mating success.—For a subset of males (13 natal males and 51 nonnatal males), data were available to examine the relationship between mating success and dispersal patterns. Estimates of male mating success were based on long-term records of sexual consortships. Most copulations took place within the context of consortships (J. Altmann, unpublished data; see also Packer 1979*b*; Smuts 1985; Bercovitch 1987; Noë and Sluifster 1990), and so consortship activity was taken as a good measure of mating success. Because male mating success varies with age in this population (J. Altmann and S. Alberts, unpublished data), we calculated age-specific levels of consort activity, then characterized each male as successful or unsuccessful relative to other males in his age class, based on whether he was above or below the median values for consortship activity for his age during each 6-mo block of time. Most males (11 of 12 nats and 43 of 51 nonnats) were consistently successful or unsuccessful (above or below the median for more than 75% of 6-mo blocks).

Male age.—Ages could be assigned to 90 males in the study. For males born into study groups, ages were based on birth dates that were known exactly ($N = 33$) or known to within 6 mo ($N = 10$). For males that first appeared in the study as subadults or adults of unknown origin ($N = 47$), birth date estimates were made on the basis of patterns of physical growth and testicular enlargement and four other physical parameters, including coat condition, degree of scarring, body carriage, and condition of canine teeth. These parameters were assessed visually by observing the animal at close range during normal activities. The scoring was developed by assessing known-age males and observing aging patterns in long-term members of the population. Resulting age estimates were used to calculate age-specific annual emigration rates (i.e., the proportion of males in each age class that emigrated yearly).

Maternal and family characteristics.—Roughly half of the males that matured in the study groups dispersed without engaging in reproductive activity in the natal group. In examining reproduction in the natal group and age at natal dispersal, we explored the effects of (1) the agonistic dominance rank of the mother at the male's conception; (2) the mother's age at the male's birth; (3) whether the mother was alive throughout the male's juvenile period, considered to be 6 yr (by that age, all males had achieved testicular enlargement, i.e., had entered subadulthood, but none had begun consorting with females or had approached adult body size); and (4) the number of sexually mature female relatives alive in the natal group by the end of the male's sixth year. None of these maternal and family characteristics were correlated with each other in this sample (e.g., mother's age and survival status, $r_s = -0.07$, $P = .67$; mother's age and rank, $r_s = -0.03$, $P = .86$).

Analysis of Failure Time Data

Throughout, we treated dispersal patterns as failure time data that were randomly censored on the right, which indicated that some males had not dispersed by the study's end or had died before dispersing (Kalbfleisch and Prentice 1980; Lee 1992). We employed survival analysis to produce (1) estimates of medians and ranges for periods of residence; (2) a survival function, representing the proportion "surviving" (in this case, the proportion not yet dispersing), for each time interval of residence; and (3) a hazard function, the conditional probability of emigrating in each time interval (Kalbfleisch and Prentice 1980; Lee 1992). Survival analyses were done in SAS, using the Lifetest procedure (SAS 1988). Two tests, the Wilcoxon test and the logrank test (SAS 1988; Lee 1992), were employed to compare survival functions and examine effects of independent variables on parameter estimates.

Seventeen males contributed multiple group tenures to the tenure length data set for nonnatal males, which raised the possibility that these multiple contributions of a few individuals influenced the parameters of the survival analysis. However, males with multiple tenures all had a wide range of different tenure lengths and in general were quite inconsistent in how long they stayed in groups (see Results and table 1). Therefore, the distribution of data for these males suggests that systematic effects of their multiple contributions were absent and that inclusion of all tenure lengths is more appropriate than any reduction of the database to a single value per male.

RESULTS

Age at Natal Dispersal and Overall Tenure Patterns for Nonnatal Males

Males dispersed for the first time at a median age of 8.45 yr, with a range of 6.81–13.42 yr (fig. 1). Sixteen males dispersed without engaging in sexual consortships in their natal group, at a median age of 7.9 yr. Nineteen males consorted in their natal group before dispersal, dispersing at a median age of 9.6 yr.

The median tenure length recorded for nonnatal males in Amboseli was 24 mo

TABLE 1
NONNATAL TENURE LENGTHS FOR MALES WITH
MULTIPLE KNOWN TENURES

Name and Group	Tenure (yr)	Age* (yr)
Aly:		
Alto's	5.7	11.0
Stud's	3.3	
Olkenya	1.9	
Stud's	.3	
Bonk:		
Olkenya	>2	8.5
Hook's	4.3	
Bor:		
Olkenya	.7	10.3
Hook's	.5	
Stud's	1.9	
Alto's	2.0	
Chui:		
Stud's	.6	8.3
Hook's	2.0	
Hans:		
Stud's	3.4	8.9
Olkenya	.5	
Hook's	1.7	
Stud's	1.1	
Hook's	.2	
Stud's	.2†	
Kaa:		
Alto's	3.5	9.8
Grendel's	3.6†	
Kojak:		
Alto's	5.7	8.25
Kojak's	5.6	
Manfred:		
Stud's	3.4	8.6
Olkenya	4.0†	
McCoy:		
Hook's	.1	10.25
Alto's	2.7	
Kojak's	2.0†	
Ozzie:		
Hook's	2.5	7.5
Stud's	3.3	
Olkenya	.6	
Stud's	.2	
Stu:		
Stud's	.3	9.25
Hook's	1.6	
Stud's	1.7	
Hook's	4.3	
Stud's	.8	
Hook's	2.3	
Vector:		
Stud's	.4	6.1
Olkenya	3.0	
Stud's	.9†	

* Denotes age at beginning of first listed tenure.

† Still resident in group at end of study.

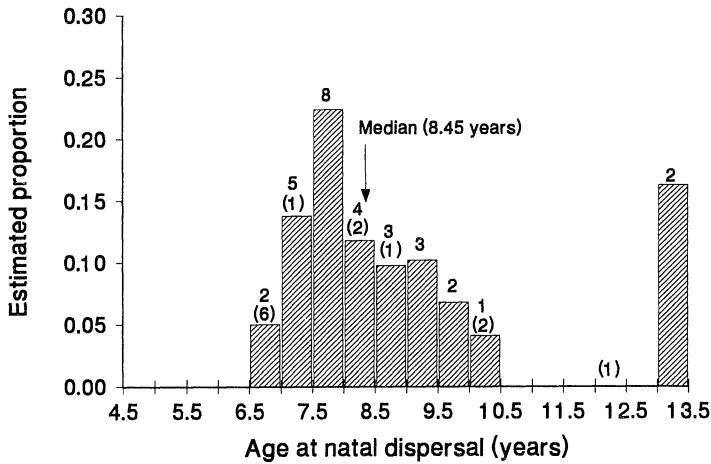


FIG. 1.—Estimated proportion of natal males dispersing in each age interval, based on a survival analysis. Numbers above bars represent a count of males known to have dispersed in each interval; numbers in parentheses represent the number of males censored in that interval (i.e., they had reached that age but had not dispersed by the end of the study).

(range, 1–138 mo). Tenure lengths ($N = 126$ tenures for 86 males) in six social groups were analyzed to produce a survival (tenure length) function (fig. 2A). Yearly hazard rates indicated that males emigrated at the highest rates in their first and sixth to eighth years of residence (fig. 2B).

Twelve males were followed for 4 yr or more as they transferred among groups in the population. Patterns of tenure for these multiteneure males were examined for trends in tenure lengths. All had at least one tenure of 2 yr or more; seven had at least one tenure of less than 1 yr (table 1). In general, these males were not consistent in how long they stayed in groups and were not significantly different from each other in their tenure patterns (single classification ANOVA, $F = 1.63$, $P > .34$).

Do Natal Males Experience Inbreeding Depression by Breeding in the Natal Group?

Of 164 conceptions in Hook's and Alto's groups between January 1980 and December 1988 (see Methods), three were behaviorally assigned solely to natal males, and 140 were assigned solely to nonnatal males (the remaining 21 had both natal and nonnatal males as likely fathers and were excluded from the analysis). Among conceptions that were solely assigned to nonnatal males, 30-d mortality was 0.19 (27 of 140). In contrast, all of the three conceptions assigned to natal males resulted in perinatal death, and in fact none resulted in live-born infants. Mortality for these three conceptions was thus 1.0. This difference was significant (G -test of independence, $G_{\text{adj}} = 7.56$, $P < .01$).

One of the three conceptions assignable solely to natal males resulted in mortality when the pregnant mother died of unknown causes, and this death may have

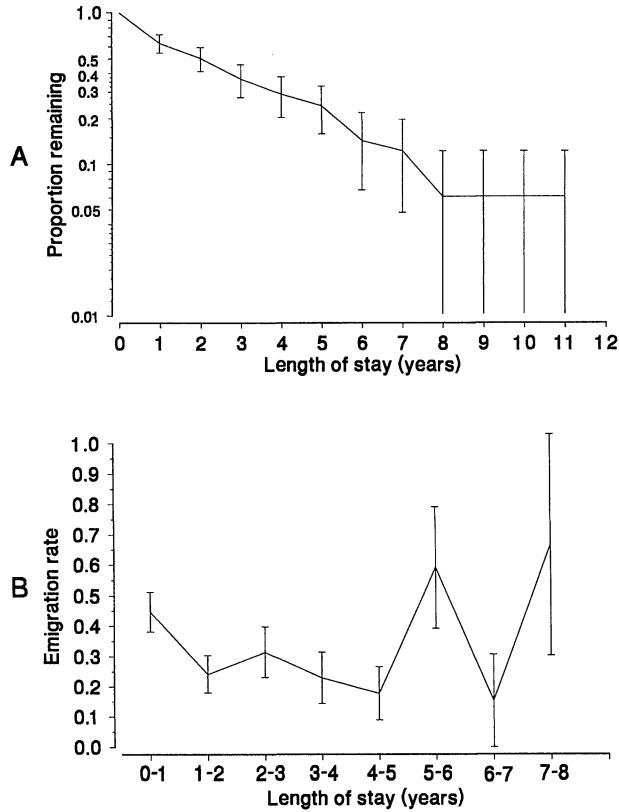


FIG. 2.—A, Log survival function with 95% confidence limits for length of stay (tenure) of males in nonnatal groups. An unspecified lower confidence limit indicates a lower limit of zero. B, Emigration (i.e., hazard) rates, with 95% confidence limits, for lengths of stay for males in nonnatal groups.

been unrelated to the paternity of the fetus. Results of our analysis did not change significantly if we excluded such cases from the sample (one among conceptions assignable solely to natal males and one among those assignable solely to nonnatal males; $G_{\text{adj}} = 4.58$, $P < .05$).

Of the 19 males that consorted in their natal group, eight had female maternal relatives undergoing reproductive cycles while the male was sexually active (four males had cycling mothers, six had cycling sisters, and two had cycling aunts or first cousins). Seven of these males never mated with their maternal relatives; all consortships between relatives were attributable to one male that consorted with his maternal first cousin. The coefficient of relatedness for this pair, considering relatedness through the maternal line only, was 0.0625. No conceptions resulted from their matings. For the pooled data across all eight males, natal males garnered 19.7% of the available consort days of females that were not their maternal relatives, and only 1.9% of the consort days of females that were their maternal relatives. A Wilcoxon signed-ranks test comparing the proportion of relatives'

TABLE 2

ESTIMATES OF MORTALITY RATES FOR DISPERSING AND GROUP-LIVING MALES

Objective	Method	Results
Estimate mortality rate for dispersing males, M_d	1. Count deaths of solitary males; calculate monthly mortality based on these counts.	.017
	2. Calculate proportion of males who died during dispersal; combine that figure with the value for the median length of time spent alone during dispersal to calculate monthly mortality.	.065
Estimate mortality rate for group-living males, M_g	1. Estimate the number of deaths of males in groups; calculate monthly mortality based on these counts.	.006
	2. Compare the known deaths of males with the known deaths of females.	.006

and nonrelatives' female consort days obtained by each natal male revealed that males consorted with their relatives in significantly lower proportions than they consorted with nonrelatives (Wilcoxon signed-ranks test, $T_S = 3$, $N = 8$, $P = .019$). We could not determine whether this clear avoidance of maternal relatives as mates was attributable to the behavior of males, females, or both.

Adult males were never observed to mount maternal relatives except in the case of the pair described above. However, natal males that had not reached adulthood (i.e., had not approached adult body size or begun consorting with females) but had undergone testicular enlargement, and presumably were capable of producing viable sperm, did occasionally mount female maternal relatives outside the context of consortships (14 of 1,934 mounts by natal males were mounts of maternal relatives outside the context of consortships). In seven of 14 cases, subadult males mounted mothers or mature sisters, and in none of these cases did the mount occur during the period in which conception is likely to occur (based on analyses in Hendrickx and Kraemer 1969). In the remaining seven cases, subadult males mounted nulliparous sisters ($N = 1$) or nulliparous maternal aunts ($N = 6$) when these young females were experiencing adolescent subfertility (Altmann et al. 1981), well before they achieved their first conceptions.

What Are the Costs of Dispersal?

The mortality cost of dispersal was estimated by comparing mortality rates of males living in groups with mortality rates of dispersing males. Two estimates of mortality for dispersing males were obtained. First, patterns of time spent alone were examined for 27 males. Estimated monthly mortality for the 418 male-months these males spent alone was 0.017. Second, by comparing the number of immigrants into ($N = 99$) and the number of emigrants out of (estimated $N = 113.3$) Alto's and Hook's groups, we estimated that 12.6% of males died during dispersal. By combining this value with the median time spent alone in this population, 2 mo (see below), we obtained a monthly mortality rate of 0.065 for dispersing males (see Methods; table 2).

In comparison, our estimate of monthly mortality rate for group-living males, based on death counts of males in groups, was 0.006. Our second estimate of mortality for group-living males, obtained by assuming that the mortality rate for group-living males is 13% lower than the female mortality rate (which is 0.007 monthly, or 0.08 yearly), was also 0.006 (see Methods; table 2).

The differences between these estimates of mortality indicate that dispersing males experience mortality rates at least twice as high as, and up to an order of magnitude greater than, those experienced by males living in groups (table 2).

Among males that were known to spend at least a day alone, the median amount of time spent as a solitary male was 2 mo; the range was 8 d–3 yr. One-quarter of the males in the sample were known to spend time alone, and periods of solitary existence are probably common among males in this population. Time spent alone results in lost reproductive opportunities: female availability varies within groups but is zero for lone male baboons, so that reproductive opportunities are never immediately improved by dispersal unless males can transfer directly into another group. This opportunity cost of dispersal may result in a substantial fitness cost for males that disperse repeatedly during their lives. Quantification of this fitness cost is complicated by the fact that it will vary greatly among males, depending on their age, dominance rank, and various other factors, and we leave to future work the exploration and quantification of this cost.

Do Reproductive Opportunities Influence Dispersal Patterns?

Nonnatal males were more likely to emigrate when the number of excess males in the group that they left was high (Kruskal-Wallis test, $\chi^2 = 8.113$, $P = .017$; fig. 3B) and to immigrate when the number of excess males in the group that they entered was low (Kruskal-Wallis test, $\chi^2 = 15.13$, $P = .0005$; fig. 3C). Similarly, natal males emigrated at higher rates when the number of excess males in their natal group was high (Kruskal-Wallis test, $\chi^2 = 8.42$, $P < .015$; fig. 3A). Both males that did and those that did not consort in the natal group conformed to this pattern.

Does Individual Mating Success Influence Dispersal?

For nonnatal males, mating success was an excellent predictor of tenure. Residence lengths of successful and unsuccessful males (see Methods) followed survival distributions that were significantly different from each other (logrank and Wilcoxon tests, $P < .0005$; fig. 4). Unsuccessful males stayed for a median of 1.2 yr and departed with an average yearly probability of 0.62, while successful males stayed a median of 4.3 yr, departing with an average yearly probability of 0.15.

Among males that consorted in their group of birth before dispersing, individual mating success was related to how long they remained in the natal group after their first consortship. Successful natal males ($N = 7$) stayed for a median of 2.7 yr and a maximum of 5.8 yr after first consortship, while unsuccessful ($N = 3$) and inconsistent ($N = 1$) natal males stayed for a median of 1 yr and a maximum of 1.7 yr. In spite of this large difference, results of statistical tests were inconclusive (logrank test, $P = .054$; Wilcoxon test, $P = .139$), which suggests that a larger sample would be required to confirm even this very large effect.

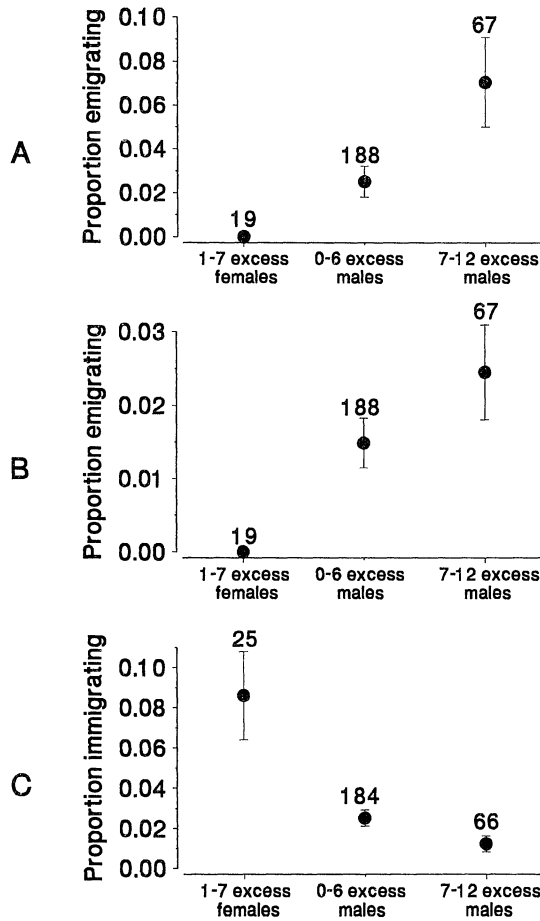


FIG. 3.—Effects of number of excess males on rate of (A) natal emigration (Kruskal-Wallis test, $P < .015$), (B) nonnatal emigration (Kruskal-Wallis test, $P = .017$), and (C) immigration (Kruskal-Wallis test, $P = .0005$). The Y-axis represents the proportion emigrating monthly. The number of excess males or females was computed as the number of adult males minus the number of cycling females. The range was from 7 excess females (equal to -7 excess males) to 12 excess males; this was divided into three categories representing high, medium, and low numbers of excess males, indicated on the X-axis by the number of excess males or females present. Numbers adjacent to the symbols on the plot indicate the number of group-months in which low, medium, or high numbers of excess males were present; bars indicate the standard error of the parameter.

Do Dispersal Patterns Change with Age?

Average rates of emigration did not differ among males of different age classes (Kruskal-Wallis test, $\chi^2 = 4.02$, $P = .67$; fig. 5A, B), but variance in emigration rate was greater for older males. Further, males that entered groups during old age exhibited a tendency to stay for shorter periods of time (logrank and Wilcoxon tests, $P < .01$), but all eight cases of males entering groups beyond 15 yr of age

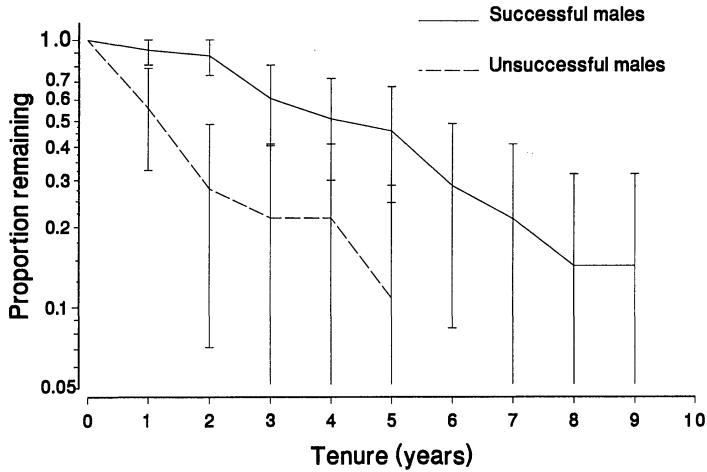


FIG. 4.—Log survival function with 95% confidence limits for successful and unsuccessful males. Males were designated as successful or unsuccessful based on whether they were above or below the age-specific median for consorting success (see text). Unspecified lower confidence limits indicate lower limits near or equal to zero.

were attributable to just three males that repeatedly entered and left groups. When these three males were excluded from the sample, age at immigration had no effect on tenure (logrank and Wilcoxon tests, $P > .15$). Nonetheless, the higher variance in emigration rates among older age classes (fig. 5B) may reflect the fact that males exhibited two different sorts of residence patterns during middle and older ages, such that males that remain resident in a single group through middle age migrated at relatively low rates during old age, while those that had not been long-term residents of a single group as they entered old age subsequently migrated more frequently. A larger sample would be required to clarify this potential pattern of heterogeneity.

Do Maternal and Family Characteristics Influence Natal Dispersal?

Neither maternal dominance rank nor the number of mature female relatives in the natal group affected age at natal dispersal. In contrast, early dispersal was associated with maternal death before the male's sixth birthday (logrank test, $P < .03$) and with having an older mother (logrank test, $P < .01$). Maternal death had its strongest effect among the earliest dispersers; all but one of the earliest dispersers were males whose mothers had died (fig. 6A). In contrast, maternal age was quite variable among males that dispersed before the median age, but almost all late dispersers had young mothers (fig. 6B).

We next examined the difference between males that consorted in the natal group before dispersal and those that did not. These two classes did not differ in the number of mature female relatives they had in the natal group or in whether the mothers survived the male's juvenile period. However, discriminant analysis

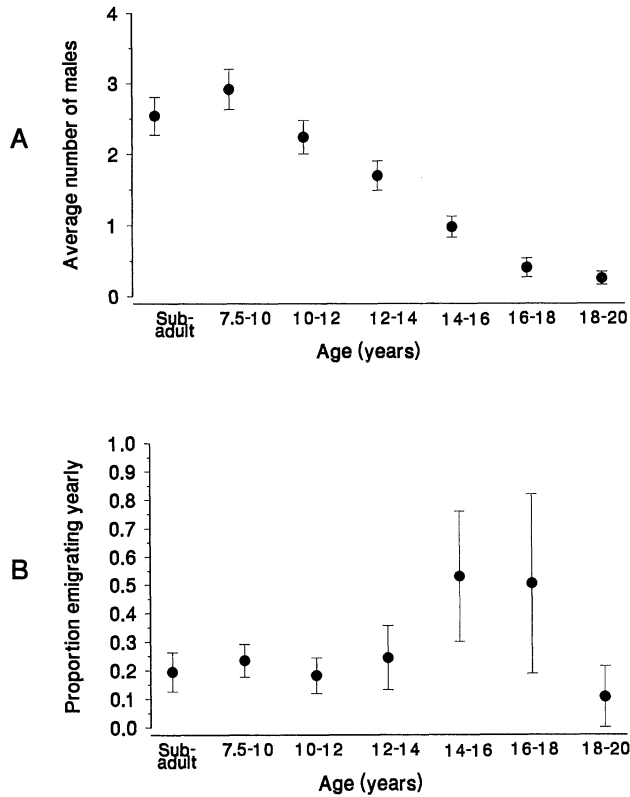


FIG. 5.—A, Average number of males in each age class yearly, \pm SE. Subadult males are males between approximately 6 and 7.5 yr of age (subadulthood is determined by physical markers of maturity rather than by age). B, Proportion in each age class emigrating yearly, \pm SE. Differences between age classes are not significant (Kruskal-Wallis test, $P = .67$).

revealed that males that consorted in the natal group tended to have younger and lower-ranking mothers than males that dispersed without consorting ($R^2 = 0.15$, $P = .01$).

Finally, eight natal males had male maternal relatives that matured at roughly the same time they did, and most had male age peers with which they matured and that were likely to be paternal brothers (Altmann 1979). In spite of the availability of potential dispersal partners, natal males never dispersed in the company of other individuals, in contrast to patterns observed among vervet monkeys in Amboseli (Cheney and Seyfarth 1983). Further, in general males were not more likely to immigrate into groups that included other members of their previous group (see Cheney and Seyfarth 1983 for contrasting data). We observed two cases of nonnatal dispersal in which males did disperse with partners. In one case, a young adult and an aged male that had resided in Hook's group together for 2.5 yr left that group on the same day and entered a nonstudy group together

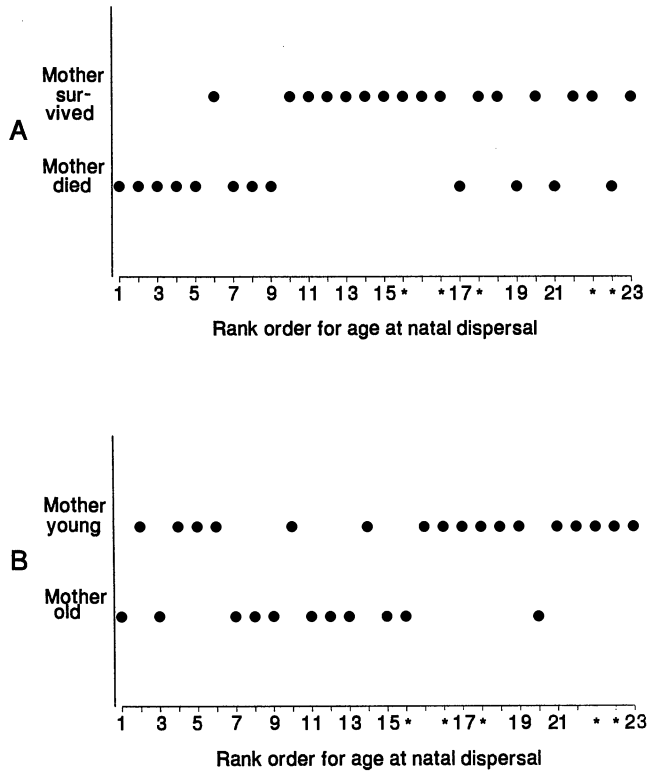


FIG. 6.—Effects of maternal survival (A) and maternal age (B) on age at natal dispersal. Rank order for natal dispersal is indicated on the X-axis; an asterisk denotes a male whose age at dispersal was censored (i.e., he had died or had not dispersed by the study's end) in the indicated interval. "Mother died" means that the mother died before the male's sixth birthday; "mother survived" means that the mother survived past the male's sixth year. "Mother old" means that the mother was more than 9 yr old (the median age for mothers in this sample) at the male's birth; "mother young" means that the mother was 9 yr or younger at the male's birth.

within 24 h. In the other case, five males all transferred from one nonstudy group to another within 6 wk of each other; at least some of these males probably transferred at the same time.

DISCUSSION

Major Features of Dispersal among Baboons in Amboseli

Three features of the dispersal patterns described here are particularly noteworthy. First, half of the natal males in this study stayed in their natal group beyond 8.5 yr of age and became reproductively active there, most with relatively high mating success. This represents a much greater proportion of males reproducing in their natal group than has been reported for other baboon populations (Pusey and

Packer 1987a). Further, despite the fact that these males did not mate with maternal relatives, our analyses suggest that males who mated in the natal group incurred a reproductive cost that was not present for males breeding in nonnatal groups.

Second, males experienced costs of dispersal in two forms. They experienced much higher mortality rates during dispersal than during group residence, and they lost opportunities to mate during dispersal because of time spent alone.

Third, female availability and individual mating success were of primary importance in determining both natal and secondary dispersal patterns. The effects of female availability on movement patterns of nonnatal males have been documented for a number of primate species (e.g., baboons: Packer 1979a; Manzollilo 1986; blue monkeys: Henzi and Lawes 1987; sifakas: Richard et al. 1992; lemurs: Sussman 1992), but the present data provide the first documentation of its effects on natal dispersal.

Changing Dispersal Patterns across the Life Span

Baboon males may disperse repeatedly throughout their lives, but influences on dispersal change as a male moves from subadulthood through old age. Our data shed light on the ways in which dispersal patterns change across three different life stages.

In Amboseli, natal dispersal was accelerated among males whose mothers had died (see Cheney 1983 for similar data on vervet monkeys) and among males with older mothers, which decreased the likelihood that they would reproduce in the natal group. In contrast, males with low-ranking mothers were more likely to mate in the natal group, even though maternal rank had no significant effect on age at natal dispersal. These maternal influences might operate directly on male behavior or indirectly by their influence on the structure of the male's family. High-ranking females in Amboseli produce more daughters than sons (Altmann 1980; Altmann et al. 1988), which suggests that sons of high-ranking females may, on the average, have more female maternal relatives, and thus fewer reproductive opportunities, than sons of low-ranking mothers. Significant differences in the numbers of female relatives were not evident for the males in this study but may nonetheless have been part of a complex array of influences on natal dispersal. Further, while none of the maternal characteristics (age, survival, and rank) were correlated with each other, some relationships between maternal characteristics and offspring numbers may warrant further study. In this sample, mothers that survived past the male's sixth birthday had more surviving offspring *younger* than the male (Spearman rank correlation, $r_s = 0.66$, $P = .0001$). Also potentially important would be a relationship in which older mothers had more surviving offspring *older* than the male, although this relationship was not statistically significant in the present sample (Spearman rank correlation, $r_s = 0.26$, $P = .13$). The presence of older siblings of either sex in the natal group may reduce reproductive opportunities there, while the presence of younger siblings may represent opportunities for increasing inclusive fitness through investment in the form of protection from conspecifics and predators. However, we found no direct effect of number of older and younger siblings on age at natal dispersal; if these influences occurred, their direct effects were undetectable in this sample.

Second, our data suggest that nonnatal males at different stages of tenure may have been influenced in their dispersal patterns by distinct factors. Emigration rates were highest during the first and sixth years of residence (fig. 2B; note that only seven of 126 tenures used in this analysis were longer than 6 yr, which precludes accurate estimates for hazard rates beyond 6 yr). The high rate of departure in the first year appears to be due entirely to the behavior of unsuccessful males, who rarely remained longer than 1 yr (fig. 4). The increase in the sixth year coincides with the period of time in which a male's first potential daughters reach maturity (Altmann et al. 1988) and suggests that, in addition to the behavioral mechanisms preventing father-daughter matings (Packer 1979a), males may tend to disperse before their daughters reach maturity (see also Pusey and Packer 1987b; Clutton-Brock 1989; Richard et al. 1992).

Third, our data show that emigration rates did not change significantly with age. However, two divergent dispersal patterns may have occurred among elderly males, one in which long-term male residents emigrated at lower rates as they aged and one in which males that were not long-term group members when they entered old age moved more frequently between groups during their senescence. Divergent dispersal patterns would account for the fact that, on the average, older males emigrated at the same rate as younger males but exhibited higher variance in that rate (fig. 5B). Most studies have reported that male transfer in primates continues well into old age (Norikoshi and Koyama 1975; Sugiyama 1976; van Noordwijk and van Schaik 1985; Richard et al. 1992; Sprague 1992), and among Japanese macaques, emigration rates appear not to change with age (Norikoshi and Koyama 1975). However, similar to what we have reported here, van Noordwijk and van Schaik (1985) reported that among wild long-tailed macaques, the small sample of males that entered groups when they were very old tended to remain in those groups for shorter periods of time.

Does Mating Success Change as Males Move between Groups?

The importance of mating opportunities in determining dispersal in this population suggests that males moved between groups as a means of improving their mating success. Further data support this view. First, data on multiple tenures of males in the study indicated that males were not consistent in their tenure lengths, staying in some groups for long periods and in other groups only briefly (table 1). These data provide indirect evidence that a male's mating success may have varied between groups, even though males tended to be consistently high or low in their mating success during any single tenure within a group. Second, data were available for a few males on consortship success in different groups ($N = 3$) or in the same group during different periods of tenure ($N = 2$). For each case in which data were available for successive tenures in different groups, males that were unsuccessful or inconsistent in the first group were successful in the second group. In no cases did males experience the same level of success during the various periods for which data were available. Accordingly, each male experienced a different level of age-specific consortship success as he moved between groups, and although this sample is small, it supports the idea that males in this population may improve their mating success by moving to another group,

in which the cohort of adult males or adult females is perhaps different enough that better mating opportunities occur.

We have shown that dispersal may result in improved mating opportunities at the same time that it presents potential fitness costs, in terms of both increased mortality risks and lost mating opportunities during dispersal. We propose a simple algebraic model that explicates the ways in which differences in population density and predation risk, through their effects on survival and mating success, might result in differences among populations of the same species in the frequency of dispersal. We examine this model in light of comparative data from different baboon populations in various habitats.

We note that although inbreeding depression may have a significant effect on fitness for matrilineal male baboons, we have not explicitly incorporated inbreeding effects in our model for several reasons. First, the variables on which we focus, while discussed in several other models, have generally received less analytic treatment than inbreeding effects, which have been explored in a number of models that have evaluated the extent to which dispersal can be explained as a mechanism for inbreeding avoidance (Bengtsson 1978; Packer 1979a; Chesser and Ryman 1986; Waser et al. 1986; reviewed in Johnson and Gaines 1990). Second, inbreeding risks change dynamically over time, partly as a result of the effects of the variables treated here, and we have not formally modeled that dynamic change, although we refer to it in our discussion. Third, because our goal was to produce a simple algebraic model with an easily visualized graphic interpretation, we chose to restrict the model to a few key variables. Finally, although inbreeding effects have not been explicitly incorporated in our model, they may be included in application by expanding our term for mating success to encompass reproductive success (including offspring survival).

A Model of Ecological Effects on Dispersal Patterns

Dispersal decisions should be driven by expected changes in survival and mating success (and implicitly inbreeding depression) that result from dispersal. These changes can be expressed as the following ratios: that of survival for dispersers to survival for those that stay (l_d/l_s), that of the proportion of time spent encountering potential mates for those that leave versus those that stay (e_d/e_s , i.e., the relative time spent in groups by dispersers compared with those that stay), and that of the number of mates attained by dispersers that survive to enter a group versus surviving stayers (m_d/m_s). Because all these processes are evaluated over the same time periods and because the ratios for dispersing versus staying males, rather than the absolute values, are considered, specification of the time units over which these processes occur is not necessary for our model. We first explore the effects of population density and predation risk on dispersal. We assume that because distances between groups are greater in low-density populations, time spent alone by males during dispersal will be an inverse function of population density. Specifically, we assume that the distance between equally spaced groups whose home ranges fill the available space in a given area will be in proportion to $1/\sqrt{N}$, where N is the number of groups, and that time spent alone during dispersal is a linear function of distance between groups. Thus,

males in low-density populations will of necessity spend more time alone on the average during dispersal.

Increased time spent alone entails two costs for dispersing males. First, it increases predation risk because lone individuals are more vulnerable to predators than are individuals in groups. As a consequence, males in low-density populations will experience greater mortality costs of dispersal. That is, at any given level of predation intensity, l_d/l_s will decrease as time spent alone increases, although in habitats with low predation rates, the slope of the mortality cost of dispersal as a function of time alone may remain low even if males spend long periods alone (fig. 7A). Second, increased time spent alone entails decreased mating opportunities, because females are not encountered outside of groups. That is, the proportion of time that a group-living male spends encountering females, e_s , is one, while the proportion of time that a dispersing male spends encountering females, e_d , approaches one for high-density populations in which males transfer directly between groups and decreases steadily as time spent alone increases. We propose that these factors are the primary determinants of the relative costs of dispersal in any given habitat and therefore that differences in dispersal rates between populations, or over time within populations, can to a considerable extent be accounted for by differences in the values of these two parameters.

However, if dispersal only entailed costs, we would not expect it to occur at all. Clearly, dispersal may also involve benefits, in the form of increased mating opportunities. In particular, we propose that the distribution of mating opportunities among groups will contribute to observed dispersal patterns such that dispersal will occur only when

$$l_d \cdot e_d \cdot m_d > l_s \cdot e_s \cdot m_s, \quad (1)$$

or, because $e_s = 1$, dispersal will occur only when

$$l_d \cdot e_d \cdot m_d > l_s \cdot m_s. \quad (2)$$

We have seen that $l_d/l_s \leq 1$ and that $e_d/e_s \leq 1$, so that dispersal will only occur when $m_d/m_s > 1$. In particular, by rearranging inequality (2), we see that dispersal will occur if and only if

$$m_d/m_s > l_s/(l_d \cdot e_d). \quad (3)$$

This model predicts that in high-density populations, in which the costs of dispersal are low, significant demographic differences between groups will be ephemeral, because males are able, at little cost, to distribute themselves across groups in direct response to changing female availability. In contrast, low-density populations will develop more demographic substructuring, because the costs of dispersal inhibit males from responding to short-term changes in within-group female availability. One probable consequence of this demographic substructuring is that, in low-density populations with low dispersal rates, more variability will exist between groups in the numbers of available females. This may tend to drive dispersal rates up by increasing m_d/m_s . Further, if dispersal rates remain low for long periods of time in such populations, levels of inbreeding within

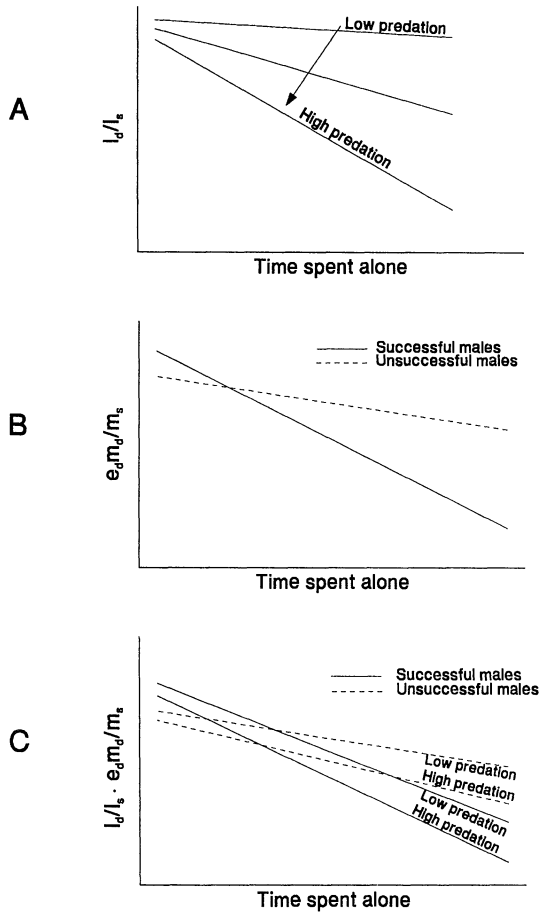


FIG. 7.—Hypothesized relationships. *A*, The ratio of l_d/l_s decreases as time spent alone during dispersal increases. Time spent alone during dispersal is an inverse function of population density. Under conditions of high predation, l_d/l_s decreases more quickly with time spent alone than it does under conditions of low predation. *B*, The relative advantage of dispersing in terms of mating success ($e_d m_d/m_s$) is higher for unsuccessful males when population density is low and time spent alone is appreciable and is higher for successful males when population density is high and time spent alone is negligible. *C*, The product $l_d/l_s \cdot e_d m_d/m_s$, which determines the probability that a male will disperse, varies, both for successful and unsuccessful males and under different conditions of predation intensity and population density.

groups will rise; if we incorporate inbreeding depression in the model, so that m encompasses offspring survival as well as number of mates or conceptions obtained, we see that inbreeding depression may tend to further increase m_d/m_s , which would thereby drive up dispersal rates as well. Thus, for any population, dispersal rates will vary between groups, as female numbers and inbreeding levels vary between groups, and will change over time, as population density, mortality risks, and inbreeding levels change.

Furthermore, consequences of these differences in demographic variability between low- and high-density populations are different for successful and unsuccessful males. In low-density populations in which time alone during dispersal is high, the opportunity cost associated with dispersal means that successful males will experience a greater relative decrease in mating success by dispersing than will unsuccessful males. In contrast, in high-density populations, both successful and unsuccessful males may escape the opportunity costs of dispersal; however, the high rates of dispersal in such populations will reduce m_d/m_s for unsuccessful males as successful males distribute themselves across groups directly in response to short-term changes in female availability (fig. 7B). That is, as the costs of dispersal change, the difference in m_d/m_s for successful and unsuccessful males reverses in sign. Further, these density-dependent effects on differences between successful and unsuccessful males will be exacerbated under high predation risk and reduced when predation risk is low (fig. 7C). That is, even under circumstances of high predation risk, an unsuccessful male may experience, on the average, an increase in expected mating success if he disperses, while under the same circumstances a successful male will experience a decrease in expected mating success with dispersal. The result would be a situation in which unsuccessful males disperse with greater frequency than successful males.

Comparing dispersal patterns of olive baboons at Gombe (Packer 1979a) with patterns at Amboseli supports the idea that differences in population density and predation risk result in different dispersal patterns. Although costs of dispersal have not been estimated for Gombe, fewer known species of predators on baboons occur there than in Amboseli, and in contrast to Amboseli no known cases of predation on adults have occurred there (Cheney and Wrangham 1987). Further, baboon density is much higher in Gombe (23 baboons/km²; Ransom 1971) than in Amboseli (1.5 baboons/km²; Samuels and Altmann 1991). Consequently, dispersing Gombe males rarely spent more than a few days living alone (Packer 1979a). Males in Amboseli, because they spent much more time living alone than did Gombe males, experienced both greater reproductive opportunity costs and higher mortality risks during dispersal than Gombe males. We suggest that these factors may explain why, in spite of the fact that males in both populations apparently experienced fitness costs by breeding in the natal group, Amboseli males frequently remained and mated in the natal group, while all Gombe males dispersed from the natal group by roughly 9 yr of age and rarely mated there. It may also explain why, at Gombe, nonnatal males with high reproductive success were more likely to transfer than those with low reproductive success, while the opposite was true in Amboseli. At Gombe, responding to short-term changes in female availability probably had few negative consequences, and males with above-average mating success apparently took advantage of these short-term opportunities to increase their access to cycling females by transferring at high rates.

Additional support comes from data on natal dispersal in *Papio ursinus* in Botswana (Hamilton and Bulger 1990). Although costs of dispersal have not been estimated for that population, predation on baboons there occurs with a frequency similar to or even higher than that observed in Amboseli (Cheney and Wrangham

1987), and a substantial proportion of males may remain to breed in their natal group (Hamilton and Bulger 1990; but see Pusey and Packer 1987*a*). Bulger and Hamilton (1988) further suggested that fitness costs associated with breeding in the natal group may be absent in that population, and this low fitness cost to remaining in the natal group may contribute to the tendency for natal males to avoid dispersal.

This model was motivated by the ecology of dispersal in baboons, and we have presented it in light of information on dispersal patterns in several baboon populations. However, the model is applicable to any group-living species in which dispersal occurs. Additional factors that influence the differential survival and reproductive success of dispersers versus nondispersers may be incorporated into this model. These might include differences between natal and nonnatal animals in mating opportunities or in offspring survival, differences in foraging efficiency between dispersing and group-living animals, or a number of other factors specific to particular species. Previous discussions of factors influencing dispersal have often sought to explain dispersal in terms of the mating advantages of dispersal compared to philopatry or of the cost of philopatry that results from inbreeding depression. We have shown that the mortality and opportunity costs of dispersal, formulated here as a function of population density and predation risk, may play an equally important role in determining how frequently individuals disperse.

Summary

The results of the current study demonstrate that baboons experience costs both of remaining in the natal group and of dispersal and that observed dispersal patterns may balance these costs. Dispersal is also influenced by competition for reproductive opportunities, and transfer between groups may result in improved mating success. The balance between these costs and opportunities varies between populations and undoubtedly contributes to the variety of dispersal patterns documented for this and other primate species. Finally, the diverse ways in which dispersal influences fitness highlights the importance of considering dispersal patterns in studies of variance in lifetime reproductive success.

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