

Are immigrant vervet monkeys, *Cercopithecus aethiops*, at greater risk of mortality than residents?

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Abstract. In general, dispersing animals are often thought to have a higher risk of mortality than their philopatric conspecifics. One possible cause for their increased risk of mortality is that dispersers move into unfamiliar areas where they are more vulnerable to predation. To examine this, mortality rates of vervet monkeys who were unfamiliar with their home ranges were compared with those of vervets who were familiar with their home ranges. Vervets who moved abruptly into unfamiliar areas as a result of group fusions had significantly greater mortality within the first 6 months than the residents they joined, and this difference decreased thereafter as the immigrants became more familiar with their new habitat. In contrast, vervets who moved into unfamiliar areas from groups that continued to exist after their dispersal suffered no greater mortality than the residents they joined. We suggest that these vervets were able to minimize their risks by timing dispersal to their advantage.

Dispersal is a widely occurring phenomenon that can have profound consequences on the genetic structure of populations (Gaines & McClenaghan 1980; Johnson & Gaines 1990). Whether animals that disperse will contribute to the genetic compositions of their new populations depends partly on their ability to survive the dispersal phase. Dispersers often face greater risks than their philopatric conspecifics, and may suffer greater mortality as a result of these risks. Such risks can include increased aggression from conspecifics (e.g. toque macaques, *Macaca simica*: Dittus 1986; howler monkeys, *Alouatta palliata*: Froehlich et al. 1981), lack of knowledge about the suitability of unfamiliar habitats (Waser & Jones 1983), and increased vulnerability to predators (e.g. prairie dogs, *Cynomys ludovicianus*: Garrett & Franklin 1988; kangaroo rats, *Dipodomys spectabilis*: Waser 1988; vervet monkeys: Isbell et al. 1990). In an earlier paper, we presented evidence that movement into unfamiliar habitats was associated with increased predation as entire groups of vervet monkeys shifted their home ranges into new and unfamiliar areas (Isbell et al. 1990). However, that

study did not unambiguously identify the relative timing of movement and predation events, nor did it control for the confounding effects of unfamiliarity and other possible characteristics of novel areas, such as habitat suitability. Here we control for these potential problems by examining mortality rates of vervets only after they dispersed into areas known to be suitable for habitation, i.e. areas in which vervets already lived.

Vervets generally live in cohesive multi-male, multi-female groups that aggressively defend the boundaries of their home ranges against incursions by neighbouring groups (Cheney 1981). They also follow the typical mammalian pattern of male-biased dispersal (Greenwood 1980): males tend to leave their natal groups and home ranges around sexual maturity (after 5 years of age) and immigrate into neighbouring groups, while females generally remain in their natal groups throughout their lives (Cheney & Seyfarth 1983).

On rare occasions, however, females have dispersed from their natal groups and home ranges and immigrated into neighbouring groups. Since the mid-1950s, one of the two main tree species in Amboseli, *Acacia xanthophloea*, has declined (Western & van Praet 1973; Western 1983; Young & Lindsay 1988), and this has been associated with

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a decline in the population of vervets that formerly used *A. xanthophloea* for both food and refuge from predators (Struhsaker 1973, 1976; Cheney et al. 1988; Isbell et al. 1990). Evidence suggests that the loss of *A. xanthophloea* trees ultimately caused the decline of the vervet population both directly through reduced reproduction (Struhsaker 1973, 1976; Cheney et al. 1988) and indirectly through increased predation. As the trees died, the largest group shifted its home range into *A. tortilis* woodlands and supplanted neighbouring groups, which shifted their home ranges away from the encroaching group. All groups moved into areas that were unfamiliar, and this movement was associated with increased predation (Isbell et al. 1990).

During this time the number of individuals in vervet groups also declined, and some groups eventually became so small that they ceased to exist as separate entities. This invariably occurred when the penultimate adult in a group disappeared and the remaining members, often including an adult female as well as immatures of both sexes, abandoned their home range and joined a neighbouring group (Hauser et al. 1986; Isbell et al. 1991). Most cases of female dispersal have occurred as a result of these group fusions.

Vervets that leave their natal groups have little or no experience in the home ranges of the groups into which they immigrate because vervet groups in Amboseli are territorial and home range overlap is minimal. If unfamiliarity with an area increases the risk of mortality (cf. Metzgar 1967; Ambrose 1972), immigrants should be expected to suffer initially higher mortality than the residents they join. This difference in mortality between immigrants and residents should also decrease over time as the immigrants become more familiar with their new home ranges. Here we compare mortality rates of residents with two classes of immigrants: animals dispersing from a familiar area as a result of group fusions, after which, the group from which they emigrated ceased to exist (fusion-immigrants), and animals dispersing from a familiar area from groups that continued to exist after their emigration (normal immigrants).

METHODS

Three groups of vervets were monitored continuously in Amboseli National Park, Kenya, from

1977 to 1988, while three additional groups were monitored continuously from 1983 to 1988. All births, deaths, injuries, apparent illnesses and disappearances were noted for each of the groups. Because vervets are relatively small and Amboseli has numerous predators and scavengers, we rarely found evidence of the cause of death when vervets died. More often they simply disappeared, often overnight. Whenever an individual disappeared, the surrounding area was searched for signs of predation, and neighbouring groups were checked for possible immigration. Indirect evidence (see Isbell 1990; Isbell et al. 1990 for details) suggests that most vervets died of predation; at least 69% of all deaths of adult females and immatures could be attributed to predation (Cheney et al. 1988). In addition to the six main study groups, up to eight neighbouring groups were censused semi-annually except in 1981.

To control for variation in rates of predation and age-related vulnerability to predation among groups, we compared only the mortality rates of similarly aged immigrants and residents within the same groups. Using data from all individuals whose histories were known, we compared mortality rates of 12 female and immature fusion-immigrants with those of 24 female and immature residents in the five groups that the immigrants joined (Table I), and the mortality rates of eight immature male normal dispersers between 2.5 and 5 years (no males have been known to transfer before 2.5 years of age; Cheney 1983a) with those of 23 similarly aged residents in the four groups that the immigrants joined (seven males, 11 females, and five individuals of unknown sex). All juvenile males and all juvenile females were included in the analyses. We did not include adult males, the largest class of dispersers, because it is difficult to distinguish between disappearances of adult males due to mortality and secondary immigration to unknown groups (cf. Isbell 1990; Isbell et al. 1990). None the less, they may face similar risks when they move into unfamiliar areas.

Mortality rates were calculated at 6-month intervals beginning on the date the immigrant joined the new group. In the comparison of fusion-immigrants and residents, immigration events occurred twice in two groups. Three residents were alive during both immigration events, and three immigrants of the first immigration event were considered as residents during the second immigration event (see Table I). Double-counting might increase the probability of

Table I. Comparison of sexes and approximate ages of fusion-immigrants with those of residents

Immigrant	Sex	Age	From group	To group	Resident	Sex	Age
RM	F	A	11	C	CY	F	A
PA	F	I			AC	F	A
					AU	F	A
					LO	F	A
					AO	F	I
					CZ	F	I
					AR	M	I
					CO	M	I
BT	F	I	10	2	CS	F	A
BE	F	I			LI	F	A
					JR	F	I
PR	M	I	4	2	LI	F	A
					JR	F	A
					BT	F	A
					BE	F	A
					NS	F	I
BA	F	A	A	1	FO	F	A
SO	F	I			LV	F	A
EG	M	I			SV	F	A
PG	M	I			LA	F	I
ET	F	A	5	C	CY	F	A
QU	F	I			PA	F	A
EE	F	I			BH	F	I
					NR	M	I
% Females	75				% Females	87	
% Immatures	76				% Immatures	39	

For analysis, the mortality of immigrants was compared with that of the residents in the group they joined. F: Female; M: male; A: adult; I: immature.

demonstrating greater mortality of immigrants relative to residents if these double-counted animals stayed alive longer than others, thereby artificially increasing the difference in mortality rates of immigrants and residents. However, during the first 6 months after the second immigration events, the double-counted residents had greater mortality (33%) than the other residents (12%). Their inclusion therefore makes the comparison between fusion-immigrants and residents more conservative than if they been excluded.

At 6-month intervals after the immigration event, we noted the proportions of immigrants and residents that disappeared within that interval and calculated the mean difference between immigrants and residents. Positive values represent greater mortality among immigrants than residents. Two-tailed *t*-tests were run on angular-transformed data (Sokal & Rohlf 1981) to determine whether these differences were statistically different from zero.

RESULTS

During the first 6 months after fusion occurred, the 12 fusion-immigrants were significantly more likely to die than the residents of the groups they joined ($t = 3.83$; $P < 0.02$; $N = 5$; Fig. 1). This difference declined in subsequent 6-month intervals. However, the eight immature male normal dispersers were not more likely to die than the immature residents of the groups they joined (first 6 months: $t = -1.00$; $P > 0.20$; $N = 5$; Fig. 2). This result did not change when we included five females who, like the immature male normal dispersers, dispersed from existing groups (first 6 months: $t = -2.04$; $0.10 > P > 0.05$; $N = 7$). Fusion-immigrants had significantly greater mortality (+30%; Fig. 1) relative to residents than did normal male dispersers (-8%; Fig. 2) in the first 6 months ($t = 3.40$; $P < 0.01$).

The greater mortality of fusion-immigrants was not simply the result of a disproportionate number

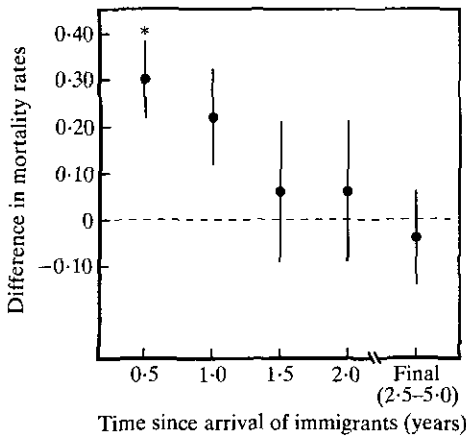


Figure 1. Differences in mean (\pm SE) mortality rates of fusion-immigrants and residents within the same group during 6-month intervals. These intervals began when the immigration event occurred and continued for 2.5 years or until the study ended. Comparisons were made on five groups for intervals 0.5 and 1.0 (years), and on four groups for subsequent intervals. The sample size decreased because one immigration event occurred less than 1.5 years before the study ended. Positive values indicate that fusion-immigrants suffered greater mortality than did residents.

*The difference in mean mortality rates of immigrants and residents was significantly greater than zero during the first 6 months after immigration occurred ($P < 0.02$). This difference decreased over subsequent intervals and was no longer statistically significant (1.0 year: $P \sim 0.10$; 1.5 years-final: $P > 0.50$).

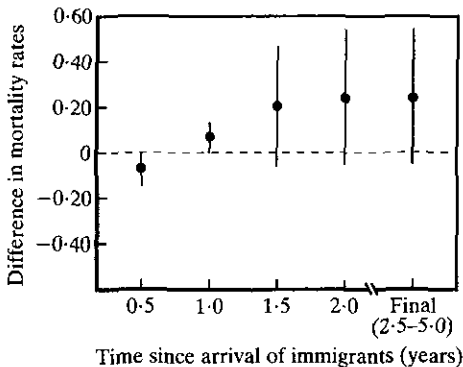


Figure 2. Differences in mean (\pm SE) mortality rates of normal male immigrants and residents within the same group during 6-month intervals. Comparisons were made on five groups for the first interval, and on four groups for subsequent intervals. The sample size decreased because one immigration event occurred in a group that was not monitored regularly after the first 6-month interval. Positive values indicate that immigrants suffered greater mortality than did residents. The mean difference in mortality rates of immigrants and residents was not significantly different from zero at any interval.

of these immigrants being immature and therefore more vulnerable to predation. Although nine of 12 (75%) fusion-immigrants were immature, immatures were not more likely to die than adult females. Only four of 17 (24%) immatures (both immigrants and residents) died during the first 6 months after the immigration events, while five of 12 (42%) adult females (both immigrants and residents) died during the same time. The greater mortality of fusion-immigrants was also not apparently the result of a sex bias toward females among fusion-immigrants. Females were not more heavily represented among the fusion-immigrants (75%) than among the residents (87%) (Table 1; $\chi^2 = 0.06$; $P = 0.80$).

DISCUSSION

Since most vervets in Amboseli die of predation (Cheney et al. 1981, 1988; Isbell 1990; Isbell et al. 1991) and no immigrants or residents died of known alternative causes (illness or wounds caused by conspecific aggression) during this time, it is likely that predation was responsible for most of the mortality among both immigrants and residents (see also Isbell 1990). We have previously shown that the movement of entire groups of adult female and immature vervets into new and unfamiliar areas was correlated with increased predation, and we suggested that this increase in mortality resulted from a lack of knowledge about the habitat (Isbell et al. 1990). The hypothesis that unfamiliarity with the habitat increases the risk of predation predicts that mortality rates of dispersers will be higher than those of residents initially and that this difference in mortality will decrease over time as immigrants become more familiar with their new home ranges. This pattern was, in fact, observed with the fusion-immigrants. However, it was not observed with the normal immigrants. That increased mortality among dispersers was not universal raises some questions about the risks of dispersal for different individuals.

Fusion-immigrants dispersed under unusual conditions. Female vervets are normally strongly philopatric; under stable conditions, they maintain home ranges with stable boundaries. Between 1977 and 1983, for example, vervet home range boundaries changed very little. Beginning in 1983, however, conditions became unstable. Some groups began shifting their home ranges into unfamiliar

areas as their former habitat deteriorated. One of these groups (group B) shifted into the territories of other smaller groups which then shifted their territories away from the encroaching group (Isbell et al. 1990). All groups maintained their integrity and attempted to defend their home ranges as long as at least two adults were present. In all cases of group fusion (listed in Table I), immigration as a result of fusion only occurred when these smaller groups were reduced to one adult and accompanying immatures. The remaining members of each of these groups immigrated by abruptly abandoning their territory within about 5 days after losing the penultimate adult in their group and joining a neighbouring group (Hauser et al. 1986; Isbell et al. 1991).

There was no evidence that lack of food as a result of ecological deterioration caused these remaining members to abandon their territories. Indeed, with fewer competitors in their groups, food should have become more available for those individuals remaining. The invariable occurrence of fusion shortly after the loss of the penultimate adult suggests instead that deterioration of the social environment determined the timing of fusions and therefore the abrupt immigration into neighbouring groups and unfamiliar areas (Isbell et al. 1991). It is possible that fusion-immigrants had no opportunity to assess their chances of successful dispersal and to time their movements accordingly. Abrupt movement into unfamiliar areas has been suggested to increase risk of mortality also in Arabian oryx, *Oryx leucoryx* (Stanley-Price 1989).

More typically, dispersing animals emigrate from groups that continue to exist after they leave. Although female vervets have been known to disperse on rare occasions, it is more common for males to disperse. In contrast to females, young male vervets often interact affinitively with members of neighbouring groups during inter-group encounters (Cheney 1981), as do young males of other primate species (e.g. chacma baboons, *Papio ursinus*: Hamilton et al. 1975; Cheney & Seyfarth 1977; olive baboons, *P. anubis*: Ransom 1981), and make forays into other home ranges prior to dispersing (Cheney & Seyfarth 1983). This may allow them to become familiar with the competitive abilities of residents, the behaviour of predators in those areas, or the locations of food and shelter, thereby reducing their risk of mortality. Those who have the option of choosing when to disperse may be better able to wait until conditions are

favourable for survival compared with those who are forced to disperse as a result of adverse conditions (see also Waser 1988). That individuals can time their movements between groups to maximize their benefits has also been suggested by the finding that immigrating adult and immature male vervets tended to assume higher ranks in their new groups than they had held in their previous groups (Cheney & Seyfarth 1983).

An alternative explanation for the higher mortality of fusion-immigrants relative to residents and the lack of such an increase in normal immigrants is that fusion-immigrants were recipients of greater aggression than residents but normal immigrants were not. While this is a possibility, evidence indicates that fusion-immigrants did not, in fact, receive higher rates of aggression or face more coalitions of aggressors than did residents (Hauser et al. 1986). Moreover, immature male normal immigrants were often targets of aggression by resident females (Cheney 1983a, b). Comparative data on aggression by adult females towards four immature natal males and three immature immigrant males during the first 6 weeks after immigration indicates that immigrant males were threatened four times as often as natal males (D. L. Cheney & R. M. Seyfarth, unpublished data). Of course, the possibility also exists that other undocumented social costs involved in immigrating to established groups may have contributed to the greater mortality of fusion-immigrants relative to both residents and immature male immigrants.

Even when entire groups moved, and therefore, their social environment did not change, an association existed between movement into new areas and increased predation (Isbell et al. 1990), suggesting that unfamiliarity with physical environments alone can contribute to short-term ecological costs of dispersal. Barring unknown social costs of immigration, this study lends support to that hypothesis, and it suggests further that predation as a cost of dispersal may depend on circumstances faced by particular individuals around the time of dispersal.

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