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Dispersal, Kinship, and Inbreeding in African Lions

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The extent of inbreeding in natural populations is often estimated by monitoring the dispersal and mating behavior of individually recognized members of a population over several generations. Such long-term studies clearly indicate that close inbreeding (between parents and offspring or siblings) is very rare in birds and mammals (reviewed by Ralls, Harvey, and Lyles 1986). In many species, sex-biased dispersal of individuals from their natal area prevents close relatives from residing together as adults (e.g., Packer 1979, Greenwood 1980, Pusey 1987). Demographic processes such as high mortality, or differential age at maturation and mortality of each sex, have the same effect (Ralls, Harvey, and Lyles 1986; Waldman and McKinnon, chapter 11, this volume). There is also considerable evidence of behavioral avoidance of inbreeding between close relatives in a variety of species (Ralls, Harvey, and Lyles 1986; Pusey and Packer 1987b).

However, it has proved much more difficult to measure from behavioral data the extent to which more moderate levels of inbreeding occur, and this has been the subject of recurrent debate (Ralls, Harvey, and Lyles 1986; Shields, chapter 8, this volume; Smith, chapter 14, this volume). Even where extensive pedigrees of local populations exist, the calculation of degrees of kinship becomes very complex because there are always some individuals breeding in the population whose origins are unknown. Pedigrees based on behavioral data must also be treated with caution because of extra-pair copulation (Rowley et al., this volume), multiple copulation (e.g., Burke et al. 1989; Rabenold et al. 1990) and intraspecific brood parasitism (Emlen and Wrege 1986).

It has recently become possible to measure levels of kinship accurately by molecular genetic techniques. DNA fingerprinting was first developed to estimate parentage (Jeffreys, Wilson, and Thein 1985;

Burke 1989), but it can also be used to estimate more distant degrees of kinship in some circumstances (Lynch 1988b, 1990; Reeve et al. 1990; Westneat 1990; Gilbert et al. 1991; Jones, Lessells, and Krebs 1991). In this chapter we show how DNA fingerprinting can be combined with other techniques to measure inbreeding in natural populations.

The lion populations of the Serengeti and Ngorongoro Crater are among the best-studied vertebrate populations in the world (Schaller 1972; Bertram 1975; Packer et al. 1988; Packer, Pusey, et al. 1991) and we have recently combined long-term genealogical data with DNA fingerprinting (Gilbert et al. 1991; Packer, Gilbert, et al. 1991). In this chapter we review lion dispersal patterns and their effect on the incidence of close inbreeding, we discuss how DNA fingerprinting can be used to measure kinship and therefore to determine relatedness between mates, and we examine the consequences of inbreeding on lion reproductive performance.

Lion Social Organization

Lions live in stable social groups ("prides") that typically contain 2–9 adult females (range: 1–18), their dependent young, and a coalition of 2–6 adult males (range 1–9) that has entered the pride from elsewhere (Packer et al. 1988). Prides are territorial and often occupy the same range for generations. Incoming males kill or evict the dependent young of the prior coalition (see reviews by Packer and Pusey 1984; Pusey and Packer 1993). Consequently, females resume sexual receptivity within days, show regular oestrus cycles for about 3 months and mate exclusively with the males of the new coalition by the time they conceive (Bertram 1975; Packer and Pusey 1983). Births tend to be synchronous within a pride (Bertram 1975) and cubs born less than 1 year apart make up a "cohort." DNA fingerprinting analysis confirmed behavioral estimates of maternity for 77 of 78 cubs (Gilbert et al. 1991). The 78th cub belonged to a female pridemate of the assumed mother. The DNA analysis also confirmed that the males of the resident coalition father all cubs born during their tenure. Males generally remain in the same pride for only 2–3 years and typically father only one cohort per pride.

Study Sites

African lions in northern Tanzania have been studied continuously since the 1960s (Packer et al. 1988, Packer, Pusey, et al. 1991). Our long-term records include data on over 2,000 individuals in two separate populations: one in the Serengeti National Park and the other in Ngorongoro Crater. These two populations differ greatly in size and extent of isolation. The Serengeti ecosystem covers 25,000 km^2, the total lion population exceeds 3,000, and males disperse over the entire region (Pusey and Packer 1987a). Over two-thirds of the 118 males that have bred in our 2,000 km^2 study area originated from other parts of the Serengeti (Packer, Pusey, et al. 1991) (figure 16.1).

In contrast, the 250-km^2 floor of the Ngorongoro Crater is a small, naturally isolated island of lion habitat. Lions have resided in the Crater for at least a century, but in 1962 an epizootic reduced the population to nine females and one male (Packer, Pusey, et al. 1991). An additional seven males apparently immigrated into the Crater in 1964–65, but there has been no further immigration in the past 25 years. The population had largely recovered by 1969 and has included 25–45 breeding animals since 1970 (figure 16.2). There was considerable variance in the reproductive success of the founders; four of five contemporary prides derive from a single group of four females, and there has been considerable exchange of males among all five prides (Packer, Pusey, et al. 1991). Hence, the Crater population is far smaller than the Serengeti population and has been genetically isolated for five generations.

LION DISPERSAL PATTERNS

Subadults of both sexes are usually forced to emigrate when their natal pride is taken over by a new coalition of males (Hanby and Bygott 1987; Pusey and Packer, 1987a). Females may also disperse when their mothers give birth to a new batch of cubs or to avoid mating with their fathers when they reach sexual maturity. About two-thirds of all female cohorts are recruited into their mothers' prides, while the remainder emigrate and establish new prides nearby (figure 16.3). Dispersing females have significantly lower fitness than females that remain in their natal pride (Pusey and Packer 1987a). Females in our study areas have never transferred successfully from one preexisting pride to another (Packer 1986; Pusey and Packer 1987a).

In contrast, almost all males leave their natal pride before the age of 4 years and undergo a nomadic phase before gaining residence in a new pride (figure 16.3). Large male cohorts often enter new prides intact, whereas cohorts of only 1–2 males may team up with singletons from other prides before gaining residence (Packer and Pusey 1982; Pusey and Packer 1987a). Small cohorts disperse farther from their natal pride than do large cohorts (Pusey and Packer 1987a). Most males

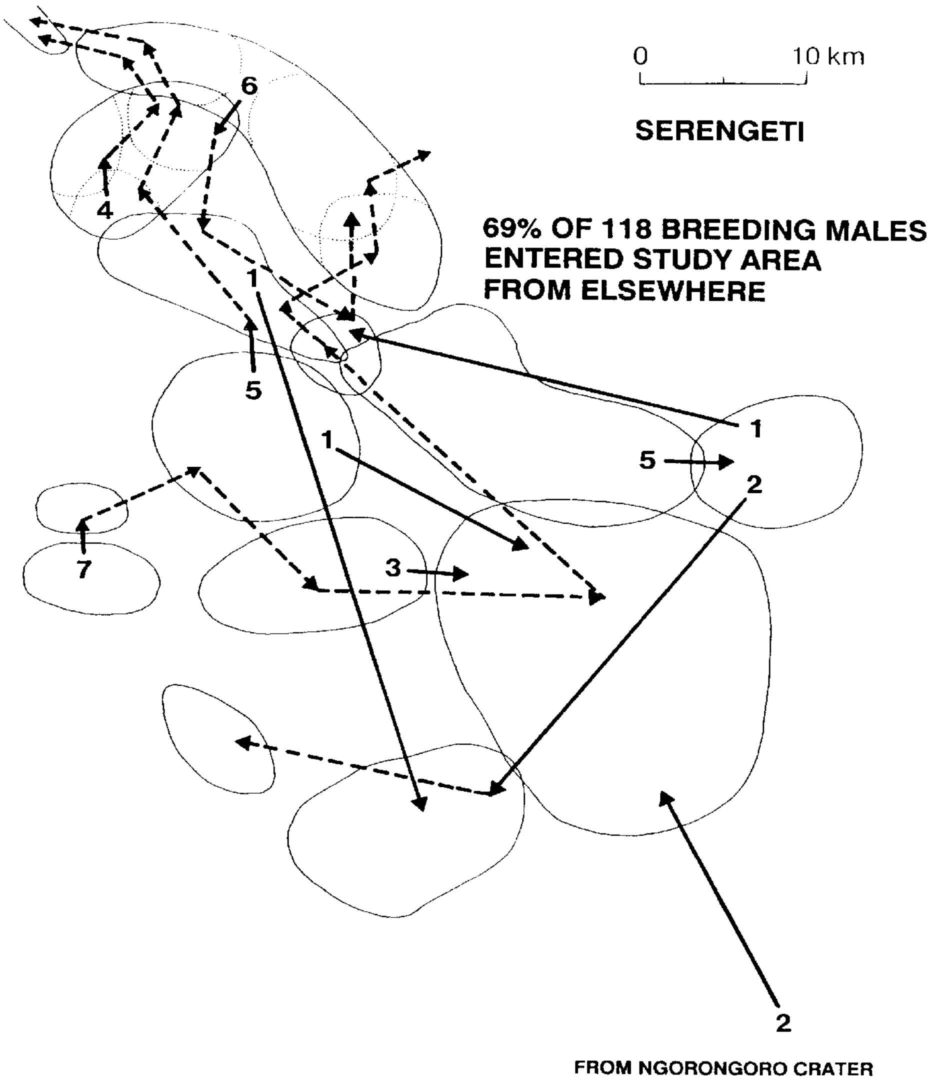

FIGURE 16.1 Size and movements of male coalitions born in the Serengeti study area that resided in study prides. Approximate pride ranges from 1974–1985 are shown. Solid arrows indicate male natal dispersal over the same period; dotted arrows indicate secondary dispersal. Note that most males resident in the study area have entered it from elsewhere. (Modified from Pusey and Packer 1987a).

in the Serengeti study population have entered the study area from elsewhere (see figure 16.1). Thus, in contrast to females, males commonly breed far from their natal range and do not appear to suffer such large losses in fitness from dispersal.

Although much male dispersal occurs as a result of eviction by usurping coalitions, some features of male dispersal apparently result from the avoidance of close inbreeding (Pusey and Packer 1987a). First, young males often disperse when they reach maturity even if their fa-

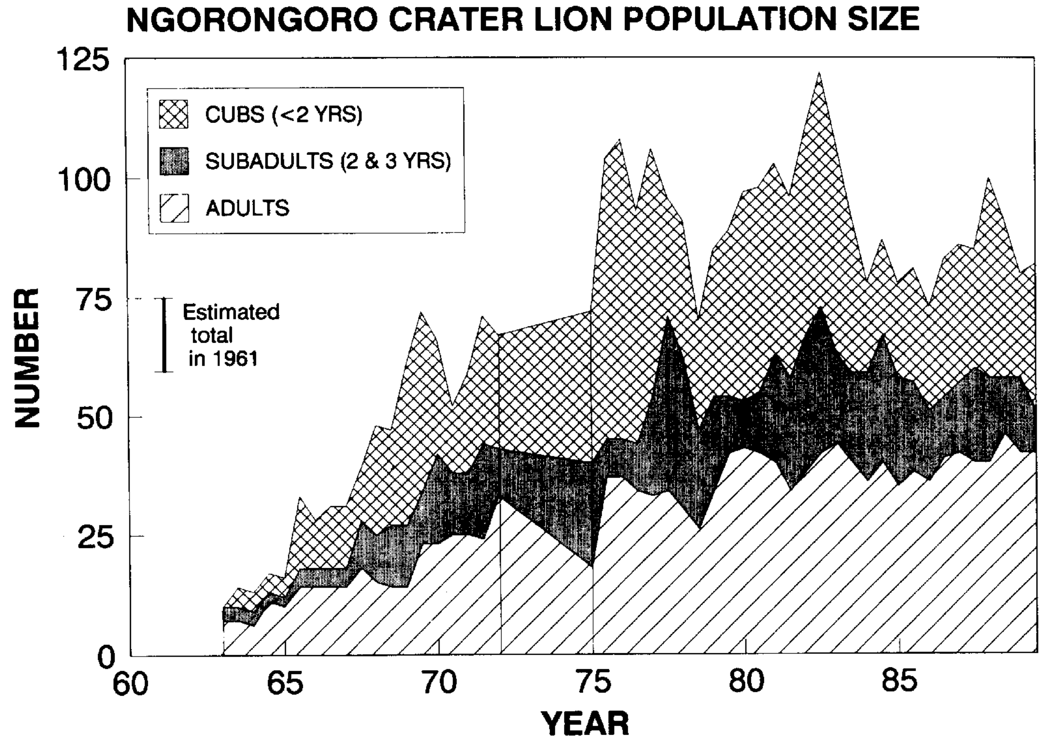

FIGURE 16.2 Population size and composition of the Ngorongoro Crater population. Data for 1961 are based on Fosbrooke's (1963) estimate. Subsequent data give the population size on 1 January and 1 July each year. For each date, the number of individuals in each age class is illustrated by the height of the respective hatched areas. Data for 1973 and 1974 are interpolated. (From Packer, Pusey, et al. 1991).

thers are still resident (although sons will team up with their fathers if they are evicted together), or even in the complete absence of adult males. Second, males almost never return to their natal pride. Third, in the Serengeti, the only two cases in which males have bred with their close relatives occurred when the males joined an offshoot of their natal pride, with whom the males were not as familiar as with their own maternal grouping. This was also true for three of four such cases in the Crater. Fourth, males never reside in the same pride as their mature daughters in the Serengeti, and rarely do so in the Crater. Vigorous coalitions of males sometimes voluntarily abandon prides containing maturing daughters for prides that contain fewer adult females. It should be noted that while the frequency with which males reside with close female relatives in the Crater is higher than in the Serengeti, the opportunity to disperse to prides containing nonrelatives is much more limited in the Crater (see also Packer, Pusey, et al. 1991).

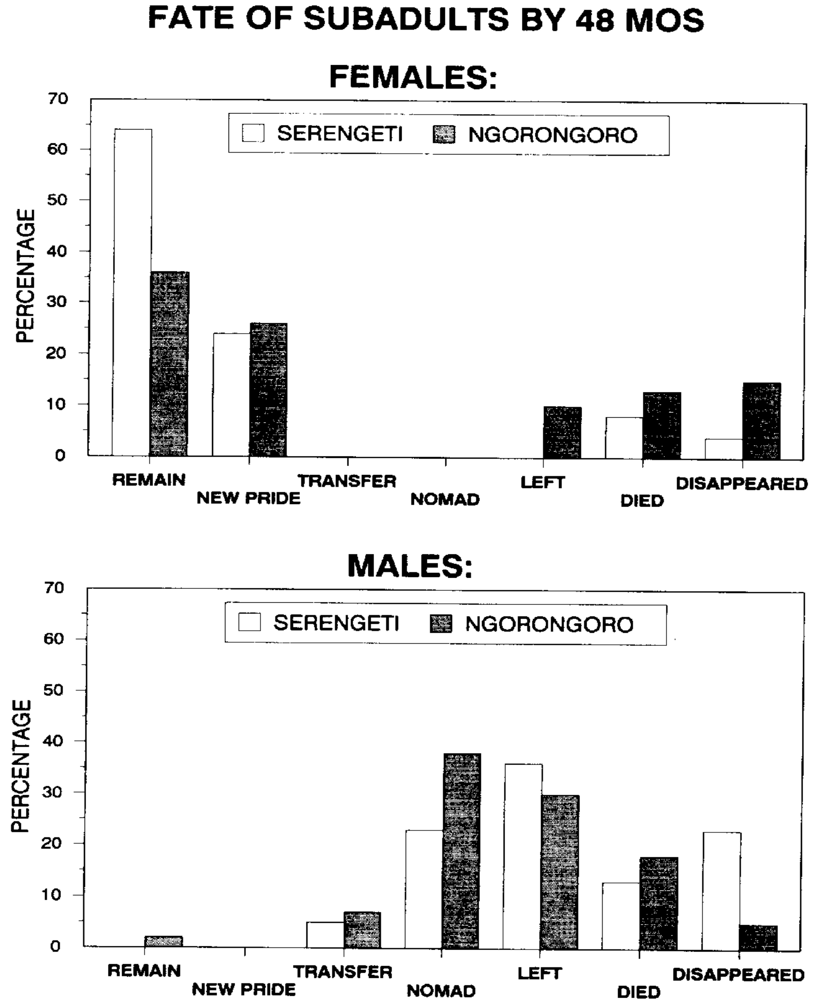

FIGURE 16.3 The fate of subadults by 48 months of age. Remain = individuals still in their natal pride. New pride = females in or adjacent to their natal range, but that no longer associate with their natal pride. Transfer = individuals that have become members of other, preexisting prides. Nomad = individuals whose range includes areas well away from their natal range. Died = individuals whose bodies were found, those last seen in very poor health, or that disappeared singly from their natal pride or cohort. Disappeared = individuals last seen in good health in their natal pride but that disappeared at the same time as at least one other member of their pride. Note that only females are considered to form new prides because males do not show a similar site specificity and male ranges depend on the ranges of the female prides in which they become resident. Data based on 280 subadults that reached 18 months of age between 1970 and 1984. (Reprinted from Pusey and Packer 1987a.)

DNA Analysis

While the demographic data indicate that close inbreeding is typically avoided in lions, it is impossible to estimate the extent to which more moderate inbreeding occurs. It has been suggested that levels of inbreeding might typically be high in populations of large vertebrates because of the limited dispersal of males (Chepko-Sade et al. 1987). Even though Serengeti males typically disperse quite far from their natal pride, there is always the possibility that any two prides are related either by previous pride splits (see below) or by past exchange of males. We have therefore employed DNA fingerprinting to measure precise relatedness between different classes of individuals in the two populations.

Using feline-specific hypervariable probes, DNA fingerprinting analysis was performed on 193 animals from the Serengeti and 23 from the Crater (Gilbert et al. 1991). The DNA was digested with restriction enzymes, and fragments were separated according to molecular weight by agarose gel electrophoresis. DNA fragments carrying different numbers of a hypervariable minisatellite repeat are visualized as bands of varying molecular weight after hybridization with a radioactive minisatellite DNA probe. These bands are inherited in a Mendelian fashion, so close relatives are expected to share more bands by common descent than unrelated individuals do. Percentage of similarity, or "band sharing," between two individuals is defined as $2F_{ab}/(F_a + F_b) \times 100\%$, where F_{ab} is the number of DNA fragments showing similar molecular weight and intensity carried by both individuals, F_a is the total number of fragments resolved in individual a, and F_b the number resolved in individual b.

Information on matrilineal kinship comes from our long-term records, which were verified by the DNA fingerprinting band-matching analysis of parentage (see above). The accuracy of these data allowed Gilbert et al. to calibrate the extent of minisatellite band sharing against a reliable independent measure of kinship. Average band sharing was calculated for known parents and offspring, known full siblings and half siblings, a variety of more distant matrilineal relatives, and individuals that came from noncontiguous prides in the Serengeti with no known kinship links.

The calibration curve differs between the two populations (Gilbert et al. 1991). In the Serengeti, the mean degree of band sharing is highly correlated with relatedness, but the relationship is not linear (figure 16.4a). The distributions of band sharing for individuals related by 0.125–0.5 overlap sufficiently to prevent classification of a particular pair of animals as siblings or cousins without independent knowledge of parentage. However, the band-sharing data readily distinguish among three classes of relationship: kin related by ≥0.125, kin related by 0.02–0.06, and nonrelatives (Gilbert et al. 1991).

The extent of band sharing also declines with decreasing relatedness

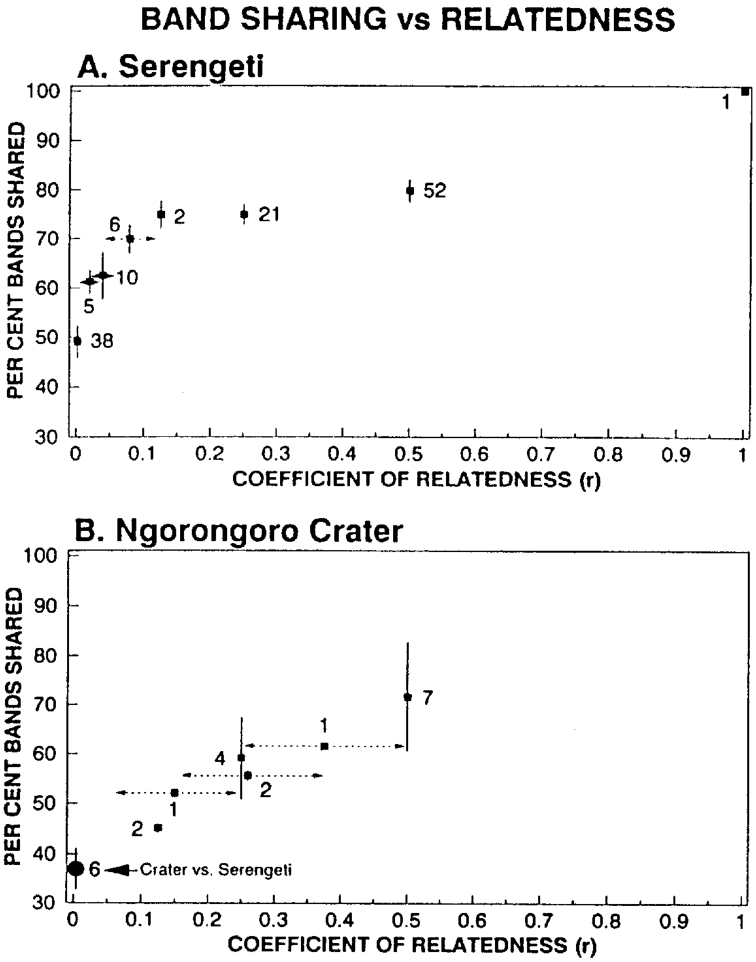

FIGURE 16.4 Calibration curves of minisatellite band sharing vs. coefficient of kinship in (a) the Serengeti population and (b) the Ngorongoro Crater population. Each point is the mean of the average percent similarity (see text) for two restriction enzymes; the vertical line is the standard deviation across the means of all comparisons in the sample. Numbers above each point are the number of comparisons in each relatedness class. For each sample, each individual in a relatedness class was compared at random to only one other individual to assure independent and equivalent weight to each individual's phenotype. Thus, for example, for first-order relatives (*r* = 0.5) in the Serengeti, there were 52 comparisons involving 104 individuals. In the Serengeti, unrelated lions were animals from different prides with no known kinship links. In the Crater, unrelated animals indicate comparison of Crater lions to Serengeti lions (see text). Both sexes were used equivalently in the calibration and there was no sex bias in band sharing. For close relatives, relatedness was known exactly from behavioral observations and pedigrees. For several more distant relatedness categories, only a range of *r* could be provided. In these cases the mean value of *r* is plotted and the range is indicated by horizontal arrows. One pair of males of unknown origins are assumed to be identical twins because they share 100% of their bands. No other kinship classifications have been made on the basis of band sharing. The Serengeti curve can only be described by a higher-order statistical analysis involving a piecemeal linear model, whereas the Ngorongoro Crater curve is linear (see Gilbert et al. 1991). All gels were scored by D. Gilbert, who did not know the genealogical relations of most individuals. (Modified from Gilbert et al. 1991.)

in the Crater population, but the relationship is more linear (figure 16.4b). Note that these estimates of *r* do not consider the history of inbreeding within the population, and that "unrelated" lions here refers to comparisons of Crater lions with those in the ancestral Serengeti population (Gilbert et al. 1991).

Although the relationship between band sharing and relatedness is expected to be linear (Lynch 1988b), the Serengeti calibration curve clearly deviates from linearity: band sharing increases much more rapidly than expected over low values of relatedness and increases only gradually at higher levels of kinship. Similar (though less extreme) nonlinearities have also been detected in other studies (Kuhnlein et al. 1990; Jones, Lessells, and Krebs 1991). One possible explanation for this pattern would be unknown kinship links between individuals assumed to be unrelated (and we had expected the calibration curve to be curvilinear in the inbred Crater population for precisely this reason). However, this cannot be the cause of the nonlinearity in the Serengeti data. First, genealogical records there are so extensive that any inaccuracies would not exceed 1–2% on average. Second, the nonlinearity is apparent within families. In ten cases, two males that were known to be unrelated to each other (and showed band sharing typical of nonrelatives: ca. 50%) each fathered offspring by the same female (to whom they also showed band sharing of only 50%). Each parent showed band sharing of 80% to their own offspring, but the band sharing between the half siblings was 74.5% ± 2.5% (Gilbert et al. 1991). If the relationship between band sharing and kinship was linear, band sharing between these half siblings should only have been about 65%.

The cause of this pattern clearly warrants further study, and data from many other populations are needed to determine how commonly such nonlinearities exist in nature. These results suggest that calibrations of kinship from band sharing should be based on at least three points (see below).

KINSHIP STRUCTURE OF LION POPULATIONS

From the behavioral data, it seemed likely that lion prides show high coefficients of relatedness between most same-sex companions but far lower relatedness between members of different prides or between mating partners (Bertram 1976). These genetic relationships could all be confirmed by the band-sharing analysis.

Kinship between Females

The minisatellite band-sharing data clearly reveal the kinship of females within and between prides. Results are presented separately for the Serengeti and the Crater because of the different relationship between kinship and band sharing in the two populations. In every Serengeti pride, female pridemates show band sharing far in excess of that found between unrelated individuals, and there is very little variation in these scores within each pride (fig. 16.5a). In spite of the more variable relationship between band sharing and kinship in the Crater, female pridemates clearly show higher band sharing than individuals from the most distantly related Crater prides (fig. 16.6a).

Figure 16.7a shows that the initial degree of band sharing between females in Serengeti prides of common ancestry is as high as within each pride, and that band sharing between prides declines through time after the prides have separated. When a cohort of daughters first splits from the parental pride, kinship ties between the two prides are as close as within each pride. But as the mothers die (maximum lifespan of females is about 17 years; Packer et al. 1988) and the separate prides recruit respective sets of daughters fathered by different coalitions of males, the degree of band sharing between prides diminishes. Many neighboring prides in the Serengeti have no known kinship links, and levels of band sharing between unrelated neighbors are as low as those between nonadjacent prides (fig. 16.7). The degree of band sharing between these prides is the same as between other nonrelatives (fig. 16.5a).

In contrast, all prides in the Crater have numerous kinship links. Most contemporary prides are descended from a founding group of four females, and there has been frequent exchange of males between all five Crater prides (Packer, Pusey, et al. 1991). Nevertheless, there is a similar decline in band sharing through time after prides split.

From the Serengeti data, it appears that most female pridemates are at least as closely related as second cousins. Such close kinship between females is consistent with the pattern of male reproductive success within each coalition and with the pattern of female dispersal. Only two males in each pride father most of the offspring (Packer, Gilbert, et al. 1991), which greatly increases the chances that any two females of similar age will be paternal siblings (Bertram 1976). Most new prides are founded by dispersing cohorts of such same-aged females (Pusey and Packer 1987a).

Kinship between Males

Levels of kinship between male coalition partners vary more than between female pridemates. Cohorts of young males remain together after dispersing from their natal pride, but singletons frequently join up with males from other natal prides (Packer and Pusey 1982; Pusey and Packer 1987a). Figure 5b shows that male coalition partners born

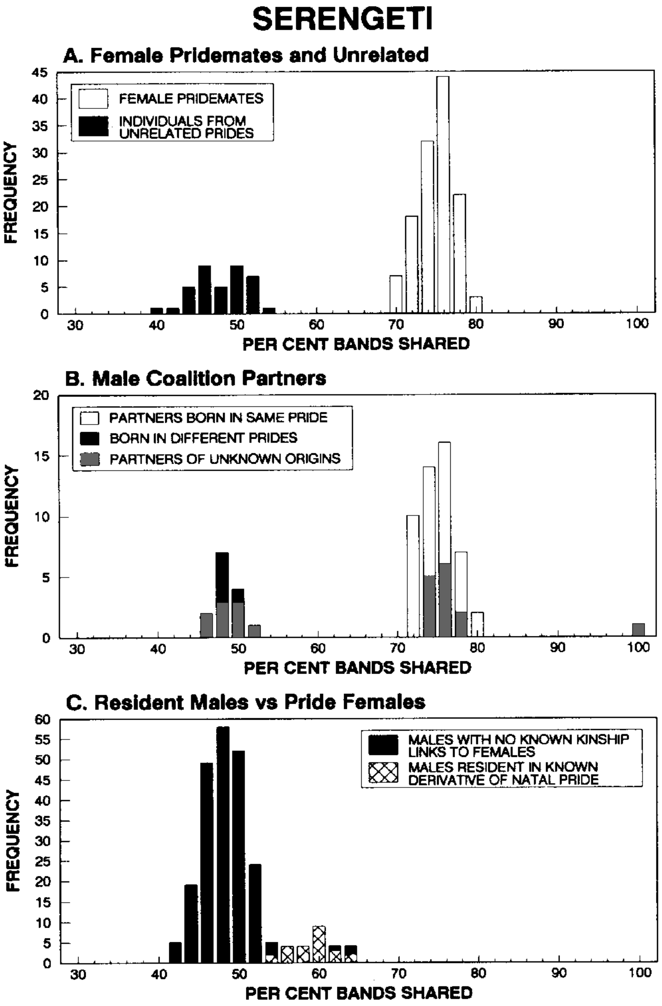

FIGURE 16.5 Frequency distributions of minisatellite band sharing within or between different classes of individuals in the Serengeti. For overlapping distributions, the number of pairs showing a particular degree of band sharing is given by the height of the respective hatched region. (Reprinted from Packer, Gilbert, et al. 1991b.) (a) Band sharing between female pridemates compared with band sharing of individuals born in different parts of the park. Data on female pridemates are based on 63 females from 15 prides and include all pairwise combinations of females within each pride (e.g., a pride of 4 females contributes 6 combinations of females). However, each unrelated individual is included in only one combination (76 different individuals in 38 pairs). (b) Band sharing between male coalition partners. Data are based on 45 males in 16 coalitions and include all pairwise combinations within each coalition. Data are plotted separately for partners known to have been born in the same pride, those known to have been born in different prides, and those that had entered the study area from elsewhere. One pair of males of unknown origins shared 100% of their bands and are hence presumed to be identical twins. (c) Band sharing between resident males and pride females. Data based on 44 males in 18 coalitions and 52 females in 15 prides, including all male-female combinations within each pride. Most males had no known kinship links to the females, but one coalition resided in a neighboring pride that derived from the males' natal pride (see text).

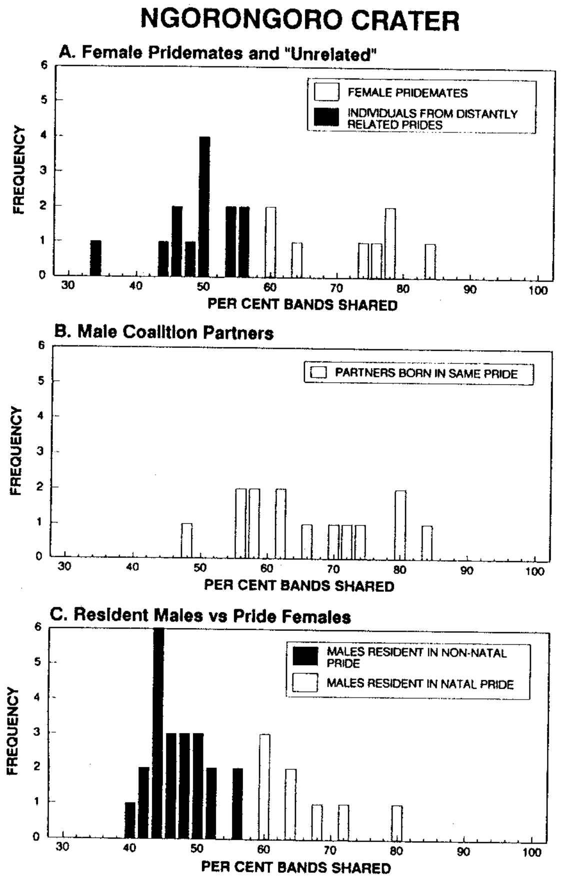

FIGURE 16.6 Frequency distributions of band sharing in Ngorongoro Crater, plotted as in figure 1. (Reprinted from Packer, Gilbert, et al. 1991.) (a) Band sharing between female pridemates (8 females in 3 prides) compared with band sharing of 22 individuals from Crater prides with the fewest kinship links. (b) Band sharing between male coalition partners (14 males in 5 coalitions). All partners were known to have been born in the same pride. (c) Band sharing between resident males and pride females (11 males in 4 coalitions and 6 females in 2 prides). All of these males became resident outside their natal pride, but members of one coalition later returned to become resident in their natal pride.

in the same Serengeti pride have the same degree of band sharing as female pridemates, whereas partners born in different prides indeed show band sharing typical of unrelated individuals. Partners in coalitions of unknown origins show a degree of band sharing that clearly belongs to one distribution or the other: a proportion of these partners

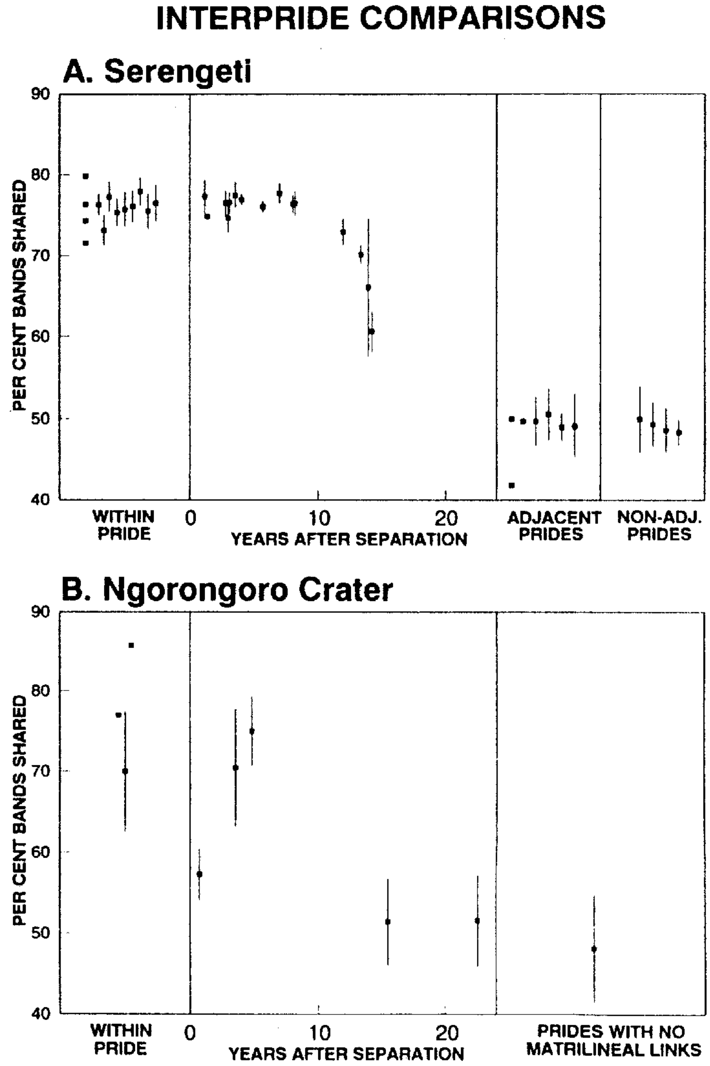

FIGURE 16.7 Degree of band sharing within and between prides. Each point represents a comparison within a pride or between two prides. Where comparisons are made between prides of common ancestry, the data are plotted against the number of years that have elapsed since the prides split apart. Data on adjacent and nonadjacent prides only include prides with no known kinship links (either through males or females) over the past 24 years. The mean and standard deviation across all pairwise combinations of individual females are plotted for each comparison. (Reprinted from Packer, Gilbert, et al. 1991.) (a) Serengeti. All comparisons involve females born in the respective prides. (b) Ngorongoro Crater. The number of between-pride comparisons was enlarged by including males as well as females born in the respective prides.

must have been born in the same pride, whereas the remainder were born in unrelated prides. In our sample from the Crater, the partners in each coalition were born in the same pride, and they show band sharing similar to female pridemates (figure 16.6b).

Kinship between Mating Partners

The band-sharing data show that resident males in the Serengeti prides are almost always unrelated to the pride females (figure 16.5c). One exceptional case concerned a coalition that gained residence in a pride that had split off from the males' natal pride 10 years before the males' births. This coalition fathered no surviving offspring in this pride and abandoned it after one year. Only one other resident male had a similar, intermediate degree of band sharing with the females of his pride. This male entered the study area from elsewhere and his kinship connections to this pride could only have been patrilineal. Even though Crater lions show less clear-cut differences in band sharing within and between prides, males resident in nonnatal prides clearly share fewer bands with the females than do males resident in their natal pride (figure 16.6c).

EFFECTS OF INBREEDING ON THE GENETICS AND REPRODUCTIVE PERFORMANCE OF THE NGORONGORO CRATER LIONS

The marked differences between the Serengeti and the Ngorongoro Crater populations in size and in extent of dispersal enable us to examine the effects of inbreeding on genetic diversity and reproductive performance. In table 16.1, we combine results from the two Tanzanian populations with data from a third, highly inbred population of captive Asiatic lions. Consistent with a history of restricted population size, the Crater lions show a significant reduction in allozyme heterozygosity and a loss of restriction fragment length polymorphism in MHC class I genes, but only a slight decrease in heterozygosity of DNA fingerprint fragments. The lions of the Sakkarbaug Zoo have a history of even more extensive inbreeding and show virtually no genetic variation.

Genetic similarity between the Crater lions and two neighboring populations suggests that the Crater population originated in the Serengeti, and simulations of the breeding history of the Crater lions predict that the average level of heterozygosity in the Crater should have declined by about 10% over the past 20 years (Packer, Pusey, et al. 1991). Thus the rather marked decrease in heterozygosity in allozymes and in the MHC may reflect a long history of repeated bottlenecks in the Crater population. The greater similarity in fingerprint diversity between the two Tanzanian populations is within the range expected from our simulations based on a single bottleneck in 1962, but may also

TABLE 16.1 Genetic and Reproductive Comparisons of Lion Populations

	Serengeti	Crater	Sakkarbaug Zoo
Isozyme polymorphism			
No. heterozygous loci/ individual	1.47	0.88	0.0
Average heterozygosity (*h*)	3.3%	2.2%	0.0
(O'Brien et al. 1987; Packer, Pusey, et al. 1991)	(*n* = 79)	(*n* = 17)	(*n* = 28)
MHC polymorphism			
Proportion of loci polymorphic	17.0%	5.8%	0.0
Average heterozygosity	21.8%	8.0%	0.0
(Yuhki and O'Brien 1990)	(*n* = 18)	(*n* = 15)	(*n* = 15)
DNA fingerprint			
Average heterozygosity	48.1%	43.5%	2.8%
(Gilbert et al. 1991)	(*n* = 76)	(*n* = 22)	(*n* = 16)
Total sperm abnormalities (%)	24.8 ± 4.0	50.5 ± 6.8	66.2 ± 3.6
(Wildt et al. 1987)	(*n* = 8)	(*n* = 9)	(*n* = 8)
Sperm mobility (%)	89.0 ± 2.1	59.0 ± 8.0	61.0 ± 3.7
(Brown et al. 1991; Wildt et al. 1987)	(*n* = 10)	(*n* = 6)	(*n* = 8)

result from the far higher mutation rates in minisatellite regions than in other regions of the chromosome (Jeffreys et al. 1988). Lions in the Crater show a higher variance in band sharing for a given coefficient of kinship (see figure 16.4), which could result from a greater degree of linkage between bands in the Crater lions.

Although the Crater population generally shows considerably lower levels of heterozygosity than the Serengeti population, direct comparisons of fertility and survival between the two populations are complicated by the very different patterns of prey availability in the two areas: the Crater lions have access to a consistently high biomass of prey, whereas the Serengeti lions are regularly subjected to serious food deprivation due to the extensive seasonal migration of their preferred prey (Schaller 1972; Kruuk 1972). Therefore cub mortality is considerably lower in the Crater than in the Serengeti (Packer et al. 1988).

Nevertheless, two lines of evidence suggest that increased levels of inbreeding impair reproductive performance in the Crater lions. First, males in the Crater have a significantly higher proportion of abnormal sperm than Serengeti males do, and the highly inbred Asiatic lions of the Sakkarbaug Zoo have even higher levels of sperm abnormality (table 16.1). In other felids, studies of in vitro fertilization show that sperm from individuals with high levels of sperm abnormality penetrate domestic cat eggs at significantly lower levels (Howard, Bush, and Wildt 1991).

Second, our estimates of average heterozygosity in the Crater over the past 25 years are closely correlated with annual reproductive rates *within* the Crater population (Packer, Pusey, et al. 1991). We used data on allele frequencies of allozymes to estimate the genetic composition of the founding population in the Crater, and then simulated the breeding history of the population using the detailed pedigrees available from the long-term study. These suggest that the overall heterozygosity of the Crater population would have declined by about 10% over the past 20 years, and reproductive performance in the Crater has showed a marked decline over the same period. Multiple regression suggests that productivity in the Crater is significantly correlated with heterozygosity as well as with the proportion of the female population that is subjected to infanticide every biennium (see Packer, Pusey, et al. 1991).

These results are consistent with data presented by Lacy, Petric, and Warneke (chapter 15, this volume) showing that mammalian reproductive performance often declines following the isolation of a small population. Because of the male immigration into the Crater in the mid-1960s, we can also test for evidence on outbreeding depression (on the assumption that the immigrant males were genetically distinct from the surviving Crater animals). Following the method of Templeton and Read (1984), we found no evidence for outbreeding depression in the Crater lions.

DISCUSSION

The demographic data clearly demonstrate that dispersal patterns result in extremely little opportunity for close inbreeding in the Serengeti lions. Although much male dispersal occurs because of male-male competition, several patterns, such as the rarity of return to the natal pride and the abandonment of prides containing maturing daughters, are best explained in terms of the avoidance of close inbreeding. The genetic data indicate that even moderate inbreeding is rare in the Serengeti. Combining data from figure 5c with our long-term records, we can confirm that resident males are typically unrelated to the females in their pride.

Demographic data indicate that levels of inbreeding are higher in the small, isolated Crater population than they are in the Serengeti (Pusey and Packer 1987a; Packer, Gilbert, et al. 1991). But even in the

Crater the incidence of close inbreeding may be rare: males only rarely breed in their natal pride, and the DNA band-sharing data suggest that males are not as closely related to their mating partners when they are resident in a nonnatal pride. The Crater population shows lower levels of heterozygosity and adverse effects of inbreeding on reproductive performance.

Molecular techniques hold considerable promise for resolving controversies over the extent of inbreeding that occurs in natural populations (see Shields, chapter 8, this volume). But it should be emphasized that the relationship between relatedness and DNA band sharing differed between the two populations. Thus the degree of band sharing should be calibrated against an independent measure of kinship (Lynch 1988b; Gilbert et al. 1991). However, it may not be necessary to use genealogical data as extensive as our own: coefficients of kinship could often be interpolated from comparisons of the degree of band sharing between parents and offspring, (r = 0.5), half-siblings (r = 0.25), and nonrelatives, as has been employed by Westneat (1990) and Jones, Lessells, and Krebs (1991). These three points might often be sufficient to indicate the overall relationship between kinship and band sharing and would also permit testing for nonlinearity in the calibration curve.

Finally, the data in table 1 emphasize the importance of combining numerous genetic techniques for studying the histories of small populations. The population history of the captive Asiatic lions has apparently resulted in the virtual loss of all genetic diversity; but the history of the Crater lions could not have been deduced from the DNA fingerprinting data alone.

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