Reprinted from: **BEHAVIOUR**

101- 4

LEIDEN
E.J. BRILL
1987

THE EVOLUTION OF SEX-BIASED DISPERSAL IN LIONS

by

ANNE E. PUSEY and CRAIG PACKER[1])
(Department of Ecology and Behavioral Biology, University of Minnesota,
318 Church St. SE, Minneapolis MN 55455, U.S.A.)

(With 8 Figures)
(Acc. 2-VI-1986)

Introduction

Sex-biased dispersal is a widespread phenomenon in birds and mammals. In most species, most members of one sex breed at or near the site of their birth while most or all members of the opposite sex disperse to their first breeding site and may disperse again between breeding efforts (GREENWOOD, 1980; WASER & JONES, 1983). Unlike birds where females disperse farther than males, in most polygynous mammals males disperse farther than females (GREENWOOD, 1980). Several explanations have been proposed for male-biased dispersal in polygynous mammals which may act singly or in combination in different species. First, females may gain greater benefits from philopatry and suffer greater costs from dispersal than males. Second, because intrasexual competition for mates is more intense among males than females, males may be forced to disperse further than females. Third, males are likely to benefit more than females from gaining access to more mates. In addition, a sex bias in dispersal decreases the likelihood of close inbreeding and this factor may reinforce the extent to which male-biased dispersal occurs. We discuss each of these factors in turn.

In polygynous mammals females invest more heavily than males in individual offspring, therefore their reproductive success is likely to be limited primarily by nutritional constraints, while male reproductive success is limited more by the number of females they can inseminate

---

[1]) We thank the Government of Tanzania for permission to conduct research and the Serengeti Wildlife Research Institute for facilities. We also thank Jeannette HANBY and David BYGOTT for valuable information, Sara CAIRNS, Monique BORGERHOFF-MULDER and Anthony COLLINS for maintaining demographic records in our absence, and Jon ROOD and Peter WASER for their comments on an early draft of this paper. This work was supported by grants from the Graduate School of the University of Minnesota and NSF grants BSR-8406935 and 8507087.

(TRIVERS, 1972; BRADBURY & VEHRENCAMP, 1977). Females might therefore benefit more than males from a detailed knowledge of food sources, refuges and denning sites, and such knowledge is probably best achieved by remaining in the natal area (*e.g.* WASER & JONES, 1983; COCKBURN *et al.*, 1985). In addition, in species where the per capita reproductive success of females increases with increasing group size, females could enhance their inclusive fitness by remaining in their natal group with their female kin, rather than joining other groups (WRANGHAM, 1980). However, since males might similarly gain from philopatry, greater advantages to females from natal philopatry would only lead to male-biased dispersal in combination with at least one of the other factors.

Intrasexual competition for mates is more intense among males than females in polygynous species and one male can often monopolise several females (TRIVERS, 1972). Therefore males are more likely to be evicted and have to disperse to find mates (CLUTTON-BROCK & HARVEY, 1976; GREENWOOD, 1980; DOBSON, 1982). Unlike the other factors, intense male-male competition by itself could lead to male-biased dispersal. WASER (1985) has developed a model in which the effects of competition can be separated from the effects of other factors.

To the extent that the reproductive success of males in polygynous species is limited by the number of mates they can inseminate, males are likely to benefit more than females by moving to groups or areas where there are larger numbers of mates (CLUTTON-BROCK & HARVEY, 1976; PACKER, 1979). However, there are factors that will constrain such movements in some species. Infanticide is widespread among polygynous mammals (HAUSFATER & HRDY, 1984). If males can prevent invading males from killing their young by guarding them, the advantages of dispersing to acquire more mates must be weighed against the costs of losing previous offspring to infanticide. Breeding dispersal in this case provides interesting parallels to models of mate desertion (*e.g.* MAYNARD SMITH, 1977). Although the acquisition of more mates can make it more advantageous to males to disperse, this factor alone is unlikely to account for the ubiquity of male dispersal in most species (PACKER, 1985).

A consequence of sex-biased dispersal is that mating between close relatives is avoided and sex-biased dispersal has been invoked as an inbreeding avoidance mechanism (*e.g.* ITANI, 1972; GREENWOOD *et al.*, 1978; PACKER, 1979; GREENWOOD, 1980; PUSEY, 1980; COCKBURN *et al.*, 1985). Since inbreeding avoidance can be achieved equally well by the dispersal of either sex, it is usually considered to act in combination with one or more of the above factors to produce the ubiquitous dispersal by males observed in most polygynous mammals (PACKER, 1979; GREENWOOD, 1980; COCKBURN *et al.*, 1985; PUSEY & PACKER, 1987). However, the extent to which sex-biased dispersal has evolved as an inbreeding avoidance mechanism, or is simply the result of sex differences in competition or other sex differences is currently the subject of debate (*e.g.* PACKER, 1979; GREENWOOD, 1980; DOBSON, 1982; MOORE & ALI, 1984; PACKER, 1985; COCKBURN *et al.*, 1985; LIBERG & SCHANTZ, 1985; DOBSON & JONES, 1986; RALLS *et al.*, 1986; PUSEY & PACKER, 1987).

In order to investigate the importance of these factors in the dispersal patterns of a particular species it is necessary to compare the causes and consequences of dispersing different distances by individuals of each sex. Such data are available for very few animals. In many mammals it is impossible to measure the benefits of philopatry or costs of dispersal to females because all females remain in their natal area (see PUSEY & PACKER, 1987). In most species it is difficult to follow the fates of males because they wander so widely. We now have sufficient data on dispersal patterns in African lions (*Panthera leo*) in northern Tanzania to be able to measure most of the costs and benefits of dispersal. Unlike many species of mammals showing male-biased dispersal, a proportion of female lions also leave their natal group, and data on the fates of dispersing individuals of each sex are thus available.

The proximate causes of subadult dispersal in lions have been described in detail by HANBY & BYGOTT (in press). Here we utilise the longterm data from two lion populations in northern Tanzania to describe the dispersal patterns of subadults and adults of each sex, concentrating particularly on the consequences of dispersal. We examine the costs of dispersal to females, and the relationship between dispersal and the maintenance of optimum group size. We examine the influence of male competitive ability in terms of group size on dispersal distance, and we investigate the extent to which males improve their access to females and provide protection for their cubs by secondary dispersal. We compare the consequences of contrasting levels of dispersal in two habitats on levels of inbreeding in their respective populations. Finally, we discuss the relative contributions of intra-sexual competition and inbreeding avoidance to patterns of dispersal in this species.

Lion social organization and optimum group size

Lions live in permanent social groups called prides that occupy stable ranges. Prides consist of a group of 2-18 females that were born in that pride, their offspring, and a coalition of 1-7 adult males that entered the pride from elsewhere (PACKER, 1986; PACKER *et al.*, in press). A proportion of females live as solitaries in stable ranges (PACKER, 1986); whereas a proportion of males live outside prides and are nomadic (SCHALLER, 1972; BYGOTT *et al.*, 1979). Prides are "fission-fusion" social units. Membership in a pride is stable but pride members are not in continuous association (SCHALLER, 1972; PACKER, 1986). Consequently, adults of the same pride often scattered in small sub-groups throughout the pride range and each adult spends a considerable amount of time alone. In our discussions of factors affecting pride size it is important to recall that this refers to the size of the social group rather than to sub-group size.

Coalitions of males compete against other coalitions to take over prides. When a new coalition takes over a pride, it evicts all the previous resident males, the male subadults, and the female subadults that are too young to conceive (PACKER & PUSEY, 1983b, 1983c; HANBY & BYGOTT, in press). They also kill or otherwise cause the deaths of all small cubs (BERTRAM, 1975; PACKER & PUSEY, 1983c, 1984). As a result, all the females become receptive, mate and produce cubs at about the same time (PACKER & PUSEY, 1983b). Females with cubs of about the same age pool them and stay in more continuous association than do non-mothers (SCHALLER, 1972; RUDNAI, 1974; PACKER, 1986). Cohorts of like-sexed cubs raised together tend to stay in or leave their natal pride together (HANBY & BYGOTT, in press).

The reproductive success of each sex depends on group size. Females living in prides containing 3-10 adult females have significantly higher per capita reproductive success than females living in smaller or larger prides, and also have higher fitness (PACKER *et al.*, in press). One reason for this pattern appears to be that very small and very large prides suffer higher rates of male takeovers and hence higher rates of infanticide. *Per capita* lifetime reproductive success of males increases linearly with coalition size (BYGOTT *et al.*, 1979; PACKER *et al.*, in press). Large coalitions are more likely to take over prides, have longer tenure in prides, and gain access to more females per male than do small coalitions.

Study areas, populations, and methods

Our study areas consist of a 2000 km² area of the Serengeti National Park, and the floor of the Ngorongoro Crater, Tanzania. The Serengeti study area lies in the south eastern portion of the Serengeti ecosystem and consists of two distinct habitats, the grassy plains to the south, and the open woodlands around Seronera. Lion density is far lower on the plains than in the woodlands because of the greater extremes in seasonal prey availability on the plains (HANBY & BYGOTT, 1979). Lions are continuously distributed over the whole

Serengeti ecosystem and the total population has been estimated at 2000-3000 (Schaller, 1972; Hanby & Bygott, 1979). The population in the Serengeti study area approximately doubled between 1966 and 1976 (Hanby & Bygott, 1979), and has since increased slightly (see Packer *et al.*, in press, for details).

Ngorongoro Crater is a volcanic caldera about 15 km in diameter lying in highlands to the south-east of the Serengeti. The Crater floor supports large populations of resident herbivores and one of the highest lion population densities in the world (van Orsdol, 1981). However, the Crater is surrounded by forest and arid scrubland which appear to support a far lower lion density than the Crater floor. In 1962 the Ngorongoro lion population was reduced from about 75 to 6-15 by a plague of *Stomoxys* biting flies following heavy rains (Fosbrooke, 1963). The population gradually returned to its former levels over the next 13 years and has since been stable at about 100 individuals (Fig. 1). Fosbrooke believed that the population recovered at least partly because of immigration into the Crater, but the lions were not individually identified and the rather slow recovery rate between 1962 and 1965 suggests that it could have resulted largely from recruitment of cubs belonging to surviving residents.

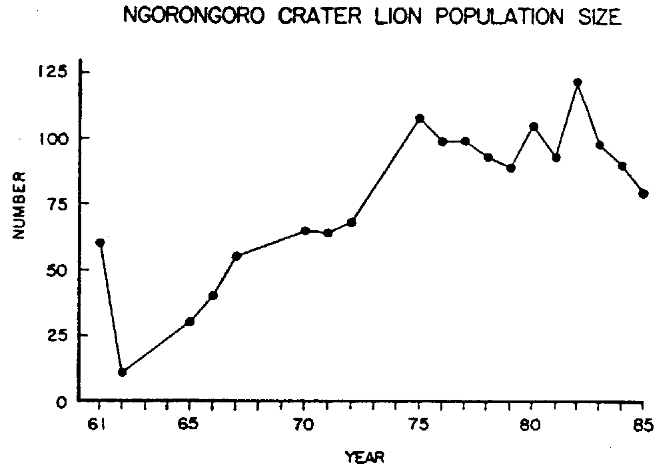

Fig. 1. Population size in Ngorongoro Crater since 1961. Data for 1961-62 are from Fosbrooke (1963), 1965-67 from Kruuk (1972), and 1970-72 from Elliott & Cowan (1978). Data from 1975-85 are from our long-term records and give the population size on July 1st of each year.

Demographic records on individually identified lions have been maintained continuously since 1966 on the descendants of two prides at the woodland edge of the Serengeti (Schaller, 1972; Bertram, 1975). The study was expanded to include all individuals living in the 2000 km² area of the Serengeti in 1974 and all the lions living on the floor of the Ngorongoro Crater in 1975 (Hanby & Bygott, 1979; Packer *et al.*, in press). Since 1978, we have maintained records on about 15 prides and three solitary females in the Serengeti, five prides and two solitary females in Ngorongoro, and all of the males that enter these areas. This totals approximately 300 individuals at any given time. We attempt to locate every resident at least once every two months, and record the location, group composition and reproductive state of each individual. All individuals can be identified by natural markings (see Pennycuick & Rudnai, 1970). Since 1984 we have radio tracked several individuals in order to follow their movements more thoroughly.

Our analysis of dispersal by subadults is based on the 148 females and 132 males born in the 20 study prides between 1973 and 1980 that survived to 18 mos of age. We also utilize data on pride fissions and male movements collected between 1970 and 1984. Subadults are defined as individuals between 18 and 48 mos of age. Although previous studies have defined subadults as 24 to 48 mos (SCHALLER, 1972; HANBY & BYGOTT, in press), many individuals leave their natal pride between the age of 18-24 mos. Females may start mating as early as 24 mos, but 4 yrs is the median age that females have their first litter (PACKER *et al.*, in press). Spermatogenesis in males begins at 26-34 mos (SMUTS *et al.*, 1978) but full weight and mane development are not usually attained until at least 4 yrs (and this is also the median age that males first become resident in a pride, see below). A "cohort" refers to subadults born less than 18 months apart in the same pride.

Results

I. Female philopatry and dispersal.

A. *Patterns of dispersal.*

Most female emigration occurs before the age of four years and Fig. 2 shows the fates of females by that age. In each study area most females have either been incorporated into their mothers' pride or have formed new prides with other members of their natal pride. There has been no case in either study area of females transferring between prides nor of females from different natal prides forming new prides. A small proportion are assumed to have died, either because they disappeared by themselves, were last seen in poor health, or their body was found. The remainder were last seen in good health and are assumed to have left the study area. Some of these were last seen outside their natal pride and are listed as having "left". The rest are listed as having disappeared, since their disappearance coincided with that of other individuals from their natal pride. Coincident disappearance is characteristic of departure from the pride rather than mortality.

In Ngorongoro, a lower proportion of subadult females remain in their natal pride and a higher proportion leave or disappear than in the Serengeti (Fig. 2). However, the number of subadults that survive until four years of age is higher in Ngorongoro than in the Serengeti (PACKER *et al.*, in press) and thus the number of females incorporated into their natal pride per year is the same in the two areas (0.4 females per pride per year). It is possible that many Ngorongoro females formed new prides just outside our study area because we can only monitor prides on the floor of the Ngorongoro Crater and the ranges of all these prides abut the Crater wall (see Fig. 5).

Emigration by adult females is less common, but adult females occasionally leave the pride with subadults, or become separated from other females of the pride when prides divide (see below).

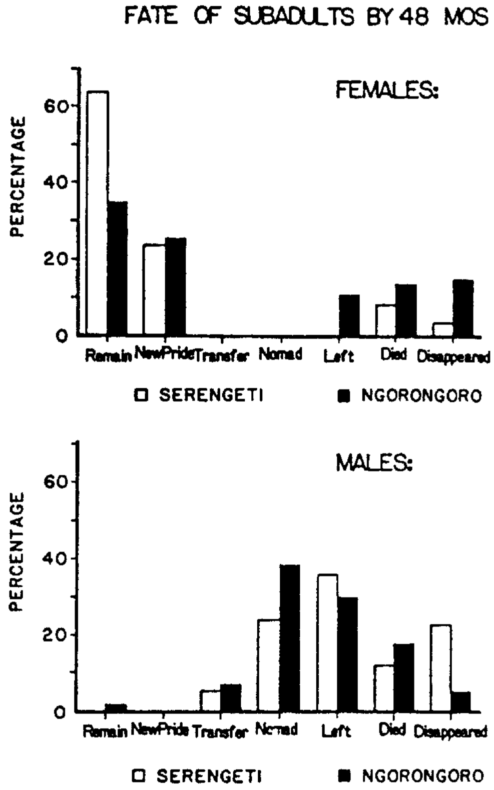

Fig. 2. The fate of subadults by 48 mos of age. Remain = individuals still in their natal pride at 48 mos. New pride = females in or adjacent to their natal range, but that no longer associate with their natal pride. Transfer = individuals that have become members of other, pre-existing prides. Nomad = individuals whose range includes areas well away from their natal range. Left = individuals last seen outside their natal pride, but no longer seen by the age of 48 mos. 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.

B. *Contexts of female emigration.*

The proximate causes of subadult emigration have been examined in detail by Hanby & Bygott (in press). Here we restrict our analysis to the contexts of emigration by females that continued to be observed in new prides or as solitaries after their departure from the original group. Table 1 provides details of all such cases of emigration by subadult and adult females. Table 1 gives the composition of the new and remaining prides after each case of emigration or fission, and the context of the event. In three cases, one adult female continued to associate with both of the

TABLE 1. Pride fissions in the Serengeti and Ngorongoro Crater. Composition of resultant prides is given in terms of subadult females (SAF) and adult females (AF). All three "link females" were adult females. Three-way splits are listed on three adjacent lines

Original pride	Year	Composition of new pride SAF	Composition of new pride AF	Link females	Composition of remaining pride SAF	Composition of remaining pride AF	Context
Serengeti							
Campsite	1975		3		9	4	Cubs?
Campsite	1984	3			1	10	Cubs
Gol	1975	2		1		3	Cubs
Kibumbu	1984	2	1			5	Takeover
Loliondo	1978	7	1	1		4	Takeover
Masai	1973	9				7	Takeover
Masai	1977	3			1	15	Takeover
Masai	1982	5				8	Takeover
Ndutu	1975	2				4	Not cubs or takeover
Sametu	1977	1			1	8	Takeover
Seronera	1973-4		2		3	3	Cubs
			2				
Seronera	1977	1				5	Cubs
Seronera	1978	3		1		4	Cubs
Simba	1979	1				6	Takeover
Ngorongoro							
Gorigor	1978	2				5	No data
Lake	1982	2			2	8	Cubs
Lake	1983		2			8	Takeover
Munge	1983	2				3	Takeover
Seneto	1976	1				4	Takeover
Seneto	1981	4				4	Cubs
Tokitok	1976	3					Avoided fathers
						2	then split
		2	1				because of cubs
Tokitok	1978	3				2	No data

resultant prides and is listed as a "link" female. Two of these died about a year after the split, but one survived longer and eventually associated only with the new pride.

New prides form in three contexts: at male takeovers, following the birth of cubs to a sub-set of the pride females, and when females mature in the presence of their fathers' coalition. When new males take over a pride, all the subadult males and most of the subadult females that are too young to conceive are evicted (HANBY & BYGOTT, in press; PACKER

& PUSEY, 1983b). Incoming males have been observed to chase out subadults of both sexes and recently evicted subadults are frequently observed with severe wounds.

Females that have been evicted at a male takeover either become peripheral and then rejoin their natal pride when they are old enough to mate, or form a new pride (HANBY & BYGOTT, in press). New prides formed at takeovers thus usually comprise only a cohort of subadults, but occasionally an adult female may accompany her daughters, or adult females with young cubs may leave the rest of the pride (*e.g.* Kibumbu pride, 1984, Lake pride, 1983, Table 1) thereby avoiding the risk of infanticide. Female emigration following the birth of new cubs shows two patterns. First, a cohort of subadults may leave and establish a new pride when their mothers have new cubs. Second, when a subgroup of adult females have cubs synchronously, they sometimes become separate from the rest of the adult females, and the pride divides (*e.g.* the 1973-4 division in the Seronera pride, Table 1). The precise cause of natal emigration by subadults in these cases is not clear. Subadult females do sometimes receive aggression from the mothers of communal litters and this may contribute to their emigration, but such subadults do not necessarily emigrate (HANBY & BYGOTT, in press; pers. obs.). When a communal litter is formed, the mothers spend far more time with each other than do non-lactating females (see above) and apparently suffer reduced food intake from being in excessively large foraging groups (PACKER, 1986). Consequently, non-mothers only rarely associate with them and may have little contact with them for up to 2 yrs, when the cubs reach the age of independence. Pride divisions sometimes (but not always) result from this reduction in contact and thus seem to be caused by a loss of familiarity between former pridemates.

For seven cohorts of females, their father's coalition was still resident in their pride after they reached sexual maturity. However, mating between females and members of their father's coalition is only rarely observed (HANBY & BYGOTT, in press) and even this is usually with the least familiar males of the coalition (see below). In such cases the females are often uncooperative with the males (pers. obs.) and we have seen females from two cohorts leave temporarily and mate with nomadic males rather than with their father's coalition. In a third case (Tokitok pride in 1976, Table 1), daughters left the pride, mated with unfamiliar males, then had cubs and did not return.

C. *Location of new prides.*

Pride ranges are stable and may persist for generations. For example, the Masai, Seronera and Loliondo prides and their descendants have occupied the same ranges for 20 years. Although the formation of new prides is fairly common, it is striking that "dispersing" females eventually settle close to their natal range. In 23 of the 24 cases of emigration or pride fission listed in Table 1, the new pride's (or solitary female's) range was either (1) entirely within the original pride range, (2) adjacent to and overlapping at least part of the original pride range, or (3) the original pride range was divided between the resultant groups. The third situation was most common when the new pride contained adult females. In the remaining case (Ndutu pride, 1975), the new pride's range was separated from the original range by a very arid and unoccupied area and was still the next adjacent pride.

Although emigrating females settle very close to their natal range they may move over large areas prior to reaching maturity. Between 1976 and 1984, several groups of emigrant subadult females in the Serengeti have been seen 30-60 kms away from their natal range, but all eventually returned and settled in or next to their natal range (BYGOTT & HANBY, pers. comm.; pers. obs.). In 1985 we radio tracked two subadult females from different prides and found that they went 30 kms and 10 kms out of their mothers' respective ranges during periods of prey scarcity, but then returned to their natal ranges. These long-range movements by subadult females give them the potential to settle in unoccupied areas far from their natal pride, but it should be noted that during the last 10 years no females have settled in either study area from outside, even though unknown subadult females are seen quite frequently in the Serengeti study area. In the few cases where ranges became available after a pride had died out, the areas were subsequently occupied by members of adjacent prides.

We have no evidence of any truly nomadic females (PACKER, 1986) and suspect that all the females in Fig. 1 that left or disappeared either died or settled immediately outside the study areas in ranges adjacent to their natal prides.

D. *Costs of dispersal.*

Female lions that left their natal prides and formed new prides suffered costs in comparison to females that remained in their natal prides, but the nature of these costs is different in the two study areas. In the

Serengeti, females that left their natal pride gave birth to surviving cubs significantly later than femaels that remained (median age of first successful breeding by cohorts of dispersed females, 94 mos, and by cohorts of non-dispersing females, 60.5 months, $U = 40$, $n_1 = 8$ emigrant cohorts that are now at least 72 mos. old, $n_2 = 22$, $P<0.05$ two-tailed)), but there was no significant difference in age of breeding among Crater females (Table 2A). In contrast, Crater females that left their natal pride were less likely to survive to eight years of age than females that remained, but there was no difference in the survival of Serengeti females (Table 2B).

TABLE 2. Costs to females from dispersal

Table 2A	Number of females whose first surviving cubs were born when she was: <48 mos of age	>48 mos of age
Serengeti:		
Remained	14 (7)	51 (16)
Dispersed	0 (0)	30 (10)
Ngorongoro:		
Remained	10 (4)	12 (4)
Dispersed	6 (3)	4 (4)

A. *Age at first breeding.* Cubs are considered to have survived if they reach 12 mos of age. Numbers in brackets show the number of cohorts in which the median female of each cohort gave birth to her first surviving cubs since females of the same cohort tend to give birth at about the same age.

Table 2B	Number of females that survived until 96 mos: Yes	No
Serengeti:		
Remained	46	2
Dispersed	25	4
Ngorongoro:		
Remained	7	0
Dispersed	5	6

B. *Survivorship.* The age at death of females from the same cohort does not show a similar statistical dependence as the age at first birth and the difference in mortality between dispersing and non-dispersing *individuals* in Ngorongoro is significant ($P<0.05$, Fisher test). There is no significant difference among the Serengeti females.

E. *Effects of pride size on the probability of dispersal by subadults.*

Per capita reproductive success of females is significantly higher in prides of 3-10 adult females than in smaller or larger prides (see above), and thus the size of the natal pride is likely to be an important factor determining whether maturing females remain or disperse. First, emigration from the natal pride should be most likely when the recruitment of a cohort of three or more subadult females would result in the pride becoming larger than 10. In such cases, the subadults would avoid being in an excessively large pride but would still be in a pride of at least three (although they would be subject to costs from dispersal). Second, cohorts of only 1-2 subadult females should show a greater tendency to remain in their natal pride since emigration would result in their living in a suboptimally sized pride. Furthermore, small cohorts should show the greatest tendency to remain when their mothers' pride would likewise fall to less than three, since it would then be in the mothers' direct interest for them to remain.

Table 3A shows that large cohorts are indeed more likely to leave when the size of their natal pride would have become greater than 10. However, four large cohorts left when their natal pride would have been 10 or less, and although their new pride was still of an "optimal" size, they

TABLE 3. Proportion of cohorts of different sizes that emigrated when their natal pride would have become either very large or very small

Table 3A	Dispersal of cohorts of three or more subadult females if their recruitment would have resulted in their natal pride becoming: 10 or less	over 10
Stay	12	1
Leave	4	5
		P<0.05, two-tailed

Table 3B	Dispersal of female cohorts of two or less if their departure would have resulted in their natal pride becoming: Two or less	Three or more
Stay	10	7
Leave	0	8
		P<0.05

Pride sizes are based on the number of females still alive when the cohort reached four yrs of age.

were presumably subject to costs from dispersal. These females left in both major contexts of dispersal (takeovers and cubs).

Small cohorts are only slightly more likely to remain than large ones, and in no case when small cohorts dispersed would the resultant pride size have been greater than 10 had they stayed. However, Table 3B shows that small cohorts are far more likely to stay when their mother's pride would otherwise have become too small. It is likely that all the small cohorts that emigrated were somehow forced to leave, but that mothers were more likely to assist their daughters in remaining when their own pride size was small. There were at least three cases where subadult females remained in their natal pride in spite of male takeovers and in one of these the subadult female was seen being chased by the new males.

Most prides are within the optimal range of pride sizes (Fig. 3), probably as a direct result of these dispersal patterns.

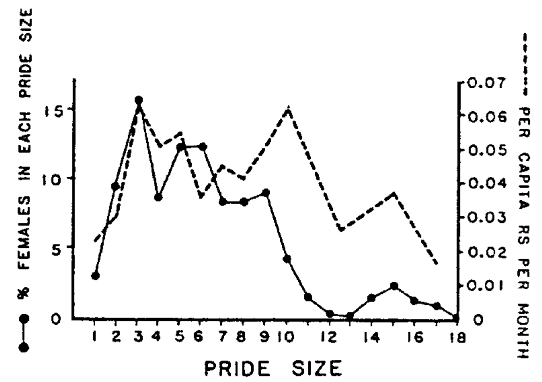

Fig. 3. Per capita reproductive success of females and the proportion of females that resided in prides of different sizes. Per capita reproductive success is the number of cubs surviving to 12 mos of age that were born each month to each female in that sized pride (data taken from PACKER *et al.*, in press). The distribution of group sizes is measured in terms of the sizes experienced by individual females (JARMAN, 1974; CLUTTON-BROCK & HARVEY, 1984). The proportion of females in each pride size is the percentage of "female months" that prides of that size existed within the study areas. Thus a pride that comprised two females for 10 mos and three females for five mos would contribute 2 x 10 = 20 female mos to the pride size of two and 15 female mos to the size of three. The percentages are based on a total of 12,087 female mos.

F. *Effects of emigration on levels of genetic relatedness in prides.*

If some of the advantages of pride membership result from cooperation with kin (see Introduction) it might be expected that the emigration patterns of females are such that they result in higher coefficients of relatedness within the resultant prides, as occurs in some primates (*e.g.*

CHEPKO-SADE & SADE, 1979). We do not have sufficient genealogical data to calculate average coefficients of relatedness of females in the prides shown in Table 1. However, we were able to calculate for each female the proportion of female pridemates to which she was related by one half (*i.e.* her mother, daughters, or probable full siblings), both prior to emigration and then in the pride in which she subsequently resided. Uterine siblings are probably full siblings because a single male usually maintains exclusive access to a female throughout her period of oestrus (PACKER & PUSEY, 1982, 1983c). The mean change in this proportion was then found across all females in each resultant pride and the signs of these changes (+ or −) are summarized separately for the emigrating and remaining groups in Table 4. In some cases, the pride split 3 ways (Table 1) and there were several new prides but only one remaining pride. In cases where a single female left her natal pride, only the effects of her departure on the remaining pride were calculated. Table 4 shows that the average proportion of pridemates that are close kin is decreased by pride splits about as often as it is increased. This is equally true in both major contexts of emigration (takeovers and cubs). In every pride fission there was at least one female that suffered a net loss in proportion of close kin, and the prides could have split in ways in which close kin would not have been separated.

TABLE 4. The effect of pride fissions on relatedness within each subsequent pride (see text)

Change in proportion of companions that are close kin	Increase	Decrease
New pride	5	5
Remaining pride	6	4

II. Male dispersal.

A. *Natal dispersal.*

1. Patterns and context of natal emigration.

Fig. 2 shows that in contrast to females, almost all males had left their natal pride by 48 mos of age. Moreover, excluding those that had died, 69% had also left the study area in the Serengeti, and 43% in Ngorongoro. Most of the remaining males had become nomads, some had taken over a new pride and only one male was still in his natal pride; and even he had departed by the time he was 49 mos old. Eleven of the males that were nomads at 48 mos subsequently became resident in other prides within the study areas.

The major context of natal emigration by subadult males is the takeover of their natal pride by new males. HANBY & BYGOTT (in press) found a highly significant correlation between the date of entry of new males and the departure of subadults.

However, male-male competition is not the only factor affecting natal dispersal of males since more males leave their natal pride than expected. The relative importance of competition can be estimated by calculating an expected proportion of cases in which individuals would be able to remain in their natal group or area given the availability of breeding "openings" (WASER, 1985). In lions, cohorts of four or more males are almost always successful at taking over new prides in competition with much smaller coalitions (BYGOTT *et al.*, 1979; PACKER *et al.*, in press). If dispersal were based on competition alone, such large cohorts would therefore be expected to remain whenever there were zero to two males resident in their pride. Since prides are controlled by such small coalitions 30.5% of the time (based on 3180 pride months of observation), a comparable proportion of large cohorts should have been able to remain in their natal pride. Instead only one of 20 large cohorts remained, which is significantly fewer than expected ($\chi^2 = 6.14$, 1 df $P < 0.02$). (The 30.5% predicts that 6.1 large cohorts would have reached the age of dispersal when there were zero to two males in the pride. This is very close to the observed number of six large cohorts that reached the age of dispersal when there were two or fewer males resident in the pride.)

Furthermore, four male cohorts emigrated when their fathers were still resident. In one case, the fathers appeared not to tolerate their sons' continued presence and chased them out; but the remaining three cohorts apparently left voluntarily, since they were last seen in amicable association with their fathers. Males can develop positive relations with their sons and may even recruit their sons into their coalition. In two cases, young males emigrated with their fathers and moved together to become residents in a new pride (see Table 5 and PACKER & PUSEY, 1982).

2. Dispersal and coalition size.

Between leaving their natal pride and taking over a new pride (if they ever succeed in doing so), many males become nomadic and wander widely (SCHALLER, 1972). In contrast to females who always disperse to adjacent areas, males sometimes reside and breed in prides far from their natal pride. During our study, a pair of males from Ngorongoro Crater

TABLE 5. Composition, age at the time of movements, and dispersal distance of male coalitions born in study prides that became resident in the study areas

Study area	Pride of origin	Natal coalition size	Number of additional companions	Age at departure	Age first resident	Months nomadic	First enter adjacent pride?
S	SW Moru	7	0	34.5	39	4.5	Yes
S	Loliondo	6	0	39	39	0	Yes
S	Sametu	5*	0	33	47	14	Yes
S	Plains	5	0	41.5	60	18.5	Yes
S	Seronera	4	0	50	50	0	Yes
N	Seneto	4	0	35	53	18	No
S	Simba	3**	0	28	46	18	Yes
N	Munge	3	0	40	51	11	Yes
S	Barafu	2	1	27	57	30	No
N	Lake	2	0	48	53	5	No
N	Seneto	2	1	22	44	22	No
N	Lake	1	2	24	53	29	Yes
S	Masai	1	2	35	61	26	No
S	Plains	1	1	41	55	14	No
S	Barafu	1	1	22	66	44	No

Natal coalition size is the number of males from the same natal pride that remained together after they left their natal pride. All natal coalitions are composed of male cohorts born in the same natal pride except those marked by asterisks: * three subadults plus both males of their father's coalition; ** one subadult plus the two surviving males of his father's coalition (which had been composed of three males at his conception). Ages in these cases are of the young males.

made at least three journeys in successive years to the Serengeti plains and back again, a distance of over 80 kms each way. During their second visit, they became resident in a Serengeti pride, were then ousted by a large male coalition and travelled a further 40 kms into the Serengeti before returning to the Crater.

Because subadult males sometimes disperse greater distances than the diameter of either study area, and over half have left or disappeared by the age of 48 mos (Fig. 2), we cannot estimate average male dispersal distance. However, by examining the movements of males that remained and bred in the study areas, we can determine the factors that influence the duration of their nomadic phase and whether or not males first reside in a pride adjacent to their natal pride.

Table 5 gives the size, composition, and age of natal dispersal for all male coalitions born in the study areas that became resident in study prides between 1970 and 1984. Figs 4 and 5 show the prides in which they were born and in which they later resided. It should be noted that during this period at least 10 coalitions born outside either study area

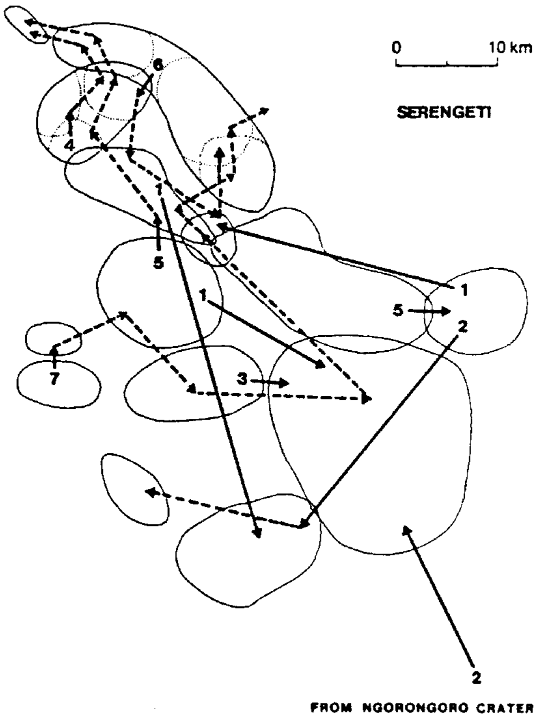

Fig. 4. Size and movements of male coalitions born in the Serengeti study area that resided in study prides. Approximate pride ranges from 1974-1985 are shown and dotted lines within pride ranges indicate the boundaries of prides that fissioned from the parent pride during that period. Solid arrows indicate male natal dispersal and dotted arrows indicate secondary dispersal. Note that natal dispersal was generally between prides that had been separate since before the start of the study.

became resident in the Serengeti study area, but no males immigrated into the Crater.

The distance that these males moved before taking over their first pride, and the age at which they did so, depended on the size of their natal coalition (see Table 5). Coalitions that first entered a pride adjacent to their natal pride were significantly larger than those that first entered non-adjacent prides ($U = 6$, $n_1 = 8$, $n_2 = 7$, $P < 0.05$). Larger natal coalitions first became resident at younger ages ($r_s = -0.62$, $n = 15$ natal cohorts that became resident, $P < 0.05$) and spent less time outside their natal pride before taking over a new pride ($r_s = -0.63$, $n = 15$, $P < 0.05$). In 6 of 7 cases where the natal coalition size was two or less, males gained additional companions before they took over their first pride, whereas coalitions of three or more never did so (Table 5). (Indeed, of all single males or cohorts of two males that left their natal pride and were observed for at least 10 months thereafter, 7 of 8 single males joined up with additonal partners, as did 4 of 7 pairs.)

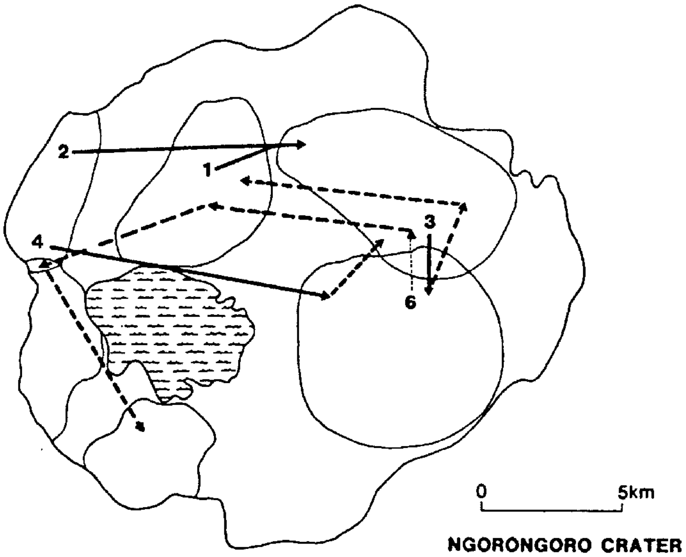

Fig. 5. Size and movements of male coalitions in Ngorongoro Crater. Solid and dotted arrows as in Fig. 4. The finely dotted arrow indicates the presumed natal dispersal of the coalition that fathered most of the individuals resident in the Crater in 1984 (see Section 11D).

However, despite the success of large coalitions, a number of large male cohorts split up permanently after emigrating from their natal pride and large cohorts appear to have greater difficulty remaining intact while nomadic than smaller cohorts. Between 1978 and 1984 there were 11 cohorts of two or more males that left or were evicted from their natal pride of which at least two members continued to be observed for at least 12 mos. Their median age at departure was 28 mos (range 18-37 mos). All five cohorts that were initially composed of 6-8 males had broken up into two or more groups within 12 mos of their emigration, whereas none of the six cohorts of 2-4 males had fragmented ($P<0.05$, runs test). A coalition of three males from an original cohort of six and four from a cohort of eight eventually took over prides within the study area. However, prior to this period, one cohort of seven males successfully remained intact and thus became the largest breeding coalition observed in the Serengeti. We do not know the initial cohort size of the other coalition of 6 listed in Table 5.

Once large cohorts have fragmented, they appear to lose familiarity with their former companions. Single males from two fragmented cohorts eventually joined up with males from other prides. One of these (MSU) joined two males from another pride and subsequently met a pair of males from his natal cohort after they had been separated for at least 15 mos. One of the pair seemed to recognise MSU and attempted to interact peacefully with him. However, MSU did not reciprocate and avoided him, and later vigorously chased the second male who was his uterine sibling.

3. Frequency of breeding in the natal pride.

Although males frequently continued to reside in their natal prides after puberty, we never observed males mating in the natal pride before they left. In both cases where young males were incorporated into their fathers' coalitions, the young males did not begin mating until they entered the new pride. Indeed there has only been one case between 1970 (when the first males of known origin became adult) and 1984, where a group of males bred with females in their natal pride before moving on to other prides (HANBY & BYGOTT, in press). By the time the males in this cohort were four yrs old, their natal pride had divided into three parts. They had spent most time as immatures with one of the resultant sub-prides and when they reached adulthood they consorted briefly with females of the second sub-pride before moving into the third and least familiar sub-pride. They fathered cubs in the third sub-pride and then left for a new pride (HANBY & BYGOTT, in press). There were no matings with their mothers or sisters. Also, in contrast to takeovers by males from other prides, small cubs in the sub-prides survived the takeover by their relatives.

It should be noted that although dispersing females have ranges adjacent to their natal pride, this is the only case in which natal males moved into an adjacent pride that was known to contain females that had originated from the males' natal pride.

B. *Secondary dispersal.*

1. Factors affecting tenure length.

Once they have taken over their first pride, male coalitions only remain resident for a few years before they are either ousted by another coalition (n = 20 departures), or relinquish their former pride in favour of another (n = 19). Figs 4 and 5 show the secondary transfers of the male coalitions that were born in the study areas. Large coalitions may reside in two or three adjacent prides simultaneously, but in some cases they abandon one pride as soon as they enter another. Simultaneous residence in several prides was most common in the Crater and the woodlands of the Serengeti where pride ranges are small.

a. Eviction *vs* voluntary departure.

The median tenure length of male coalitions in individual prides between 1966 and 1985 was only 26 mos. Those that were ousted had significantly shorter tenure lengths than coalitions that left of their own accord (ousted coalitions: median = 21 mos, range = 2-42 mos; those that left voluntarily: median = 33 mos, range = 13-90 mos; $U = 112.5$, $n_1 = 20$, $n_2 = 19$, $P < 0.05$).

Those that left voluntarily showed considerable variation in their length of residence. The offspring of these males were an average of 15 mos old when the coalitions abandoned them and the age of offspring also varied widely at the departure of different coalitions (range of average age of cubs at males' departure = 2-26 mos, n = 19 abandoned prides). In the following section we examine the factors that affect the tendency of males to abandon prides voluntarily.

b. Secondary dispersal: mate acquisition, paternal care and inbreeding avoidance.

A considerable proportion of secondary dispersal involves the voluntary movements of large coalitions between adjacent prides. These coalitions may (1) enlarge their holdings by annexing additional prides without surrendering previous prides (n = 25 cases), (2) acquire a new pride at the expense of giving up an earlier one (n = 5), or (3) relinquish some of their prides in order to spend more time with a preferred pride (n = 8).

The annexing of additional prides presents no special problems: by so doing males can acquire an additional 1-18 females. However, in the other two cases the males lose previously held females and subject their cubs to considerable risks when they abandon the pride. The coalition thus exposes the cubs to infanticide since they are no longer present to defend their young against invading coalitions. Abandoned prides are often taken over by a new coalition within a few weeks and the consequences of such a takeover depend on the age of the cubs. Fig. 6 shows that small cubs almost never survive a takeover, but by the time they reach about 16 months, their likelihood of survival has increased considerably.

The data suggest that the movements of males are sensitive to the vulnerability of their cubs. This is well illustrated in the cases where coalitions relinquished one of the prides that they had previously held simultaneously. These cases always involved males that were nearing the end of their tenure. In five cases the coalition had been reduced in size

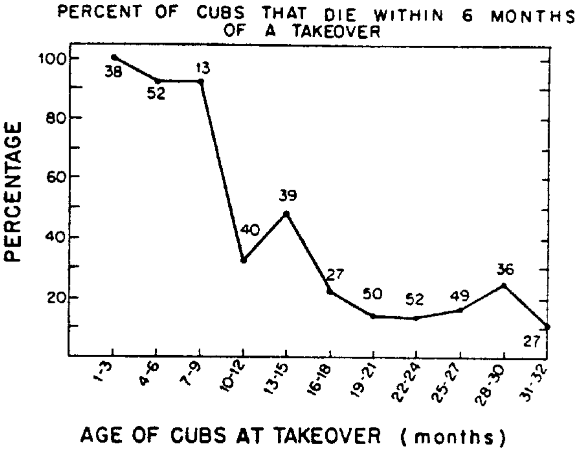

Fig. 6. Age-specific cub mortality at takeovers. The percentage of cubs of each age that died within six months of a male takeover (excluding the two cases where males took over their natal pride, see text). Numbers give sample sizes for each age.

through male mortality; and in the other three the males were approaching old age. In every case they relinquished the pride with cubs that, by virtue of their age, were least vulnerable to a subsequent takeover (Fig. 7). Neither the number of females nor the number of cubs had a significant effect.

In contrast, coalitions that abandoned one pride for another were younger and more vigorous, and they generally abandoned cubs in their previous pride. By entering a new and larger pride males of a coalition can gain more matings, but abandoning the previous pride puts previous young at risk. In these cases a choice must be made between continuing to protect their previous litters and acquiring additional matings in the new pride. Males can quickly gain more matings in the new pride since they will kill or evict all the immatures in that pride; however, their mating activity in the previous pride is limited by the long interbirth interval of females with surviving litters (median = 730.5 days, see Appendix 1).

In Appendix 1 we derive an expected curve which shows the minimum increase in number of females necessary to overcome the loss in fitness of a current batch of cubs when left unprotected. This curve incorporates the survivorship of cubs, their risk of mortality once they have been abandoned, and the interbirth interval of females with surviving cubs. When males have cubs of 10-28 mos they should be willing to abandon that pride for a new one even if the new one is smaller. Cubs of 10-28 mos have a good chance of surviving a subsequent takeover but most of

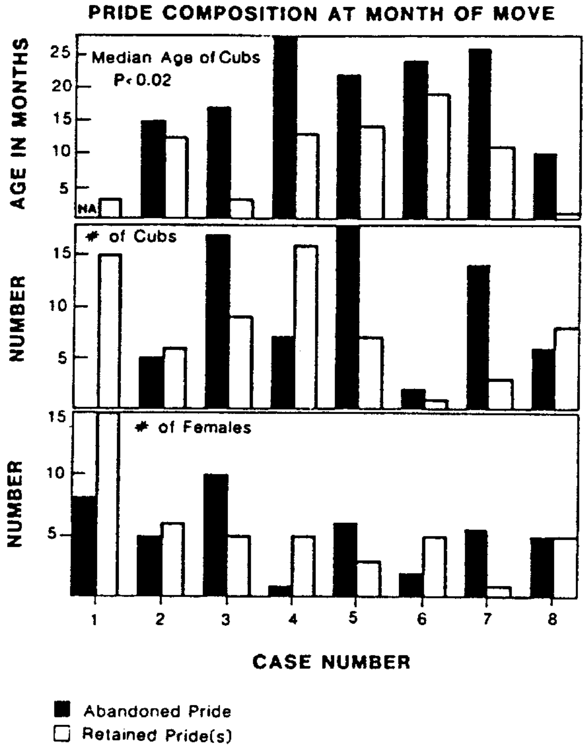

Fig. 7. The median age of cubs, number of cubs, and number of females in abandoned prides compared to prides that were retained by male coalitions. Coalitions showed a significant tendency to retain prides with younger cubs (P = 0.016, sign test); but showed no tendency to retain prides with either more cubs or females.

their mothers have not yet resumed breeding. At all other ages, males should only abandon their cubs if they thereby acquire more females. Before cubs are 10 months old they require protection by their fathers to survive. After cubs are 28 months old, most mothers have resumed sexual activity and are ready to breed again.

Fig. 8 shows the observed relationship between age of cubs and females gained or lost by the five coalitions that abandoned one pride for another. Although males that abandoned small cubs did gain sufficient females to overcome the loss of these cubs, both coalitions that left for new prides when their cubs were approaching 24 mos went to far smaller prides than expected. In these latter cases, the males had daughters that were reaching sexual maturity in the pride. In one case there would have been 12 daughters in that pride, in the other there would have been five. (Note that no effect of inbreeding was incorporated into the expected distribution).

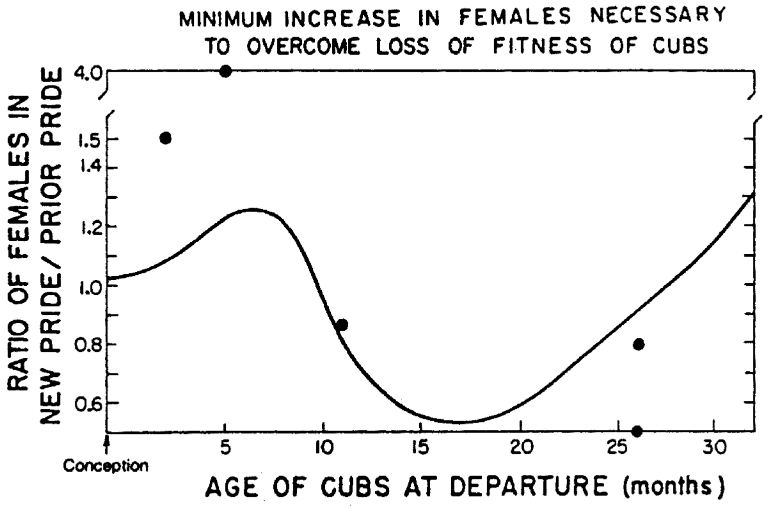

Fig. 8. The relative increase in numbers of females necessary to overcome the loss of fitness of cubs at each age. The line represents the minimum ratio of females in a new pride compared to a prior pride that males would have to gain to achieve an overall increase in fitness if the cubs in the previous pride were consequently exposed to a takeover. The minimum is generated by the model in Appendix 1; and observed values should all lie above that line. The solid dots show the change in numbers of females that five male coalitions experienced when they abandoned one pride for another (see text).

Males in the Serengeti always left prides before their daughters started mating. Only in the Crater did males sometimes remain after their daughters had matured, and most of these cases were due to one coalition of six males that resided in four of the five Crater prides. This coalition held several prides simultaneously and it is striking that even these males modified their ranging patterns as their cubs matured. Males of this coalition that had spent the most time with a particular pride when daughters were conceived began to associate more consistently with other prides as their probable daughters matured.

2. Return to the natal pride.

Although most large coalitions reside in several prides over the course of their lives, few return to their natal pride and most move progressively away from it (Figs 4 and 5). The only exception in the Serengeti involved a set of males that took over an offshoot of their natal pride five years after they had left it. All of the females in this pride had been born after the males had left and hence were completely unfamiliar to them. One set of males in the Ngorongoro Crater returned and bred in their natal pride after they had become resident in an adjacent pride. Several adult females and cubs permanently left the pride at the takeover, but others (including a uterine sibling of the males) remained and mated with them. However, matings during the females' cycle of conception were not seen, so we cannot be absolutely sure that these males were the fathers of the cubs born during their tenure in their natal pride: daughters avoid their resident fathers and the sister might have similarly avoided her brothers (see Section I.B.). As in the case of males breeding in their natal pride before leaving, small cubs present in the pride survived this takeover.

C. *Costs of dispersal to males.*

Since all males disperse eventually it is impossible to measure the costs of dispersal as was done for females; or even to estimate the costs of dispersing different distances since dispersal distance is so strongly affected by competitive ability as determined by group size. Male mortality is higher than female mortality at the age of male natal dispersal (PACKER *et al.*, in press), but we cannot separate the effects of dispersal *per se* from those of male-male competition.

The mortality of males when their coalition successfully takes over a new pride is not higher than in other circumstances. Only one male in 47 died in the same month that his coalition took over its first pride and one male of 88 died when his coalition made a secondary move.

D. *Environmental factors affecting male dispersal and levels of inbreeding.*

The Ngorongoro Crater lion population is very much smaller than the Serengeti population (*ca* 100 *vs* *ca* 2000-3000) and the two populations show differences in large-scale dispersal patterns (Figs 4 and 5). In the Serengeti, many males born in the study area left it, and many others entered the area from outside and bred there (Section II.A.2). In contrast, although a proportion of males and females leave the Ngorongoro Crater, there has been no immigration of either sex into the Crater since continuous individual identification of the lions began in 1975. The areas surrounding the Crater are thought to support only a very low density of lions (see Study Areas), and these few probably originated from the Crater. Resident prides occasionally move up the Crater walls and we therefore assume that many of the subadult females in Fig. 2 whose fates were unknown established themselves in the highlands. Therefore, even if there was some immigration following the *Stomoxys* plague in 1962 (see Fig. 1), this was probably by lions that originated from the Crater floor.

In the Serengeti study area, at least half the breeding males present during the study period originated from outside. In contrast, all the males breeding in the Crater over the last 7 yrs are thought to have originated there. Indeed, since 1978 a group of six males that was probably born in the Tokitok pride (H. VAN LAWICK, pers. comm.) has been resident in the other four prides for 2-7 yrs and these males are the presumed fathers of all the other breeding males in the Crater. They are also presumed to be the fathers of 61% of the 28 adult females in the Crater and the grandfathers of another 11%. We do not know the relatedness of these six males, but at least some of them are likely to be brothers since such large coalitions are invariably composed of males from the same natal cohort.

III. Costs of close inbreeding.

Because of the general isolation of the Crater population, the apparent genetic bottleneck following the *Stomoxys* plague, and the restricted number of breeding males in the past 7 yrs, the Crater lion population is clearly more inbred than the Serengeti population. We can therefore compare the two populations for evidence of costs from close inbreeding. Ngorongoro lions have significantly lower levels of heterozygosity and Ngorongoro males have smaller testes, higher incidence of sperm deformities and lower testosterone levels than their Serengeti counterparts (WILDT *et al.*, 1986). Comparable physiological data on females have not yet been collected. Cub survival is higher in the Crater but this is due to the far higher levels of food availability in the Crater than the Serengeti (PACKER *et al.*, in press).

Although a comparison of these two populations reveals detrimental effects of inbreeding, we cannot provide reliable data with which to look for evidence of inbreeding depression *within* populations. Observations of mating are too infrequent to provide reasonable estimates of paternity and the available data also suggest that females avoid mating with their close male relatives. Thus data from prides where resident males are closely related to females of that pride can not provide a reliable indication of the level of inbreeding in the pride. For the record, however, we did examine the reproductive performance of females in Ngorongoro whose father or brothers were resident in their pride when they conceived. In all cases of possible father-daughter matings, there were six males in the male coalition when the daughters were conceived and we do not know which was the father. These females had slightly lower cub survival than females of the same age whose close male relatives were not resident (56% *vs* 63%) and had slightly smaller litters (2.43 *vs* 2.50). However, neither result is statistically significant.

Discussion

All the factors outlined in the Introduction appear to contribute to the male-bias in dispersal in lions. We discuss the importance of each of these in turn and, where appropriate, contrast males with females.

Female philopatry and dispersal.

Female lions, like females in many other mammalian species (*e.g.* GREENWOOD, 1980; WASER & JONES, 1983; PUSEY & PACKER, 1987) show a very strong tendency to remain and breed close to the site of their birth. The majority of females remain in their natal group, and almost all the rest remain in or near their natal range. The fact that emigrating females eventually settled within or adjacent to their natal range, even after ranging widely, suggests that it is easier to settle close to the natal range than elsewhere. Nevertheless, females in these new prides suffered costs from leaving their natal pride. Those in the Serengeti suffered from a delay in first reproduction, as has also been found in dispersing female red howlers (*Alouatta seniculus* (CROCKETT, 1984) and brown bears (*Ursus americanus*) (ROGERS, 1977), and those in the Crater suffered higher mortality.

We do not know the causes of these costs, but at least two factors may be involved: the advantages of familiarity with an area, and the advantages of having neighbors who are close relatives (WASER & JONES, 1983). It seems likely that familiarity with an area might be important to successful cub rearing. Females would be most familiar with good denning sites or areas of good hunting in their natal range and several females are known to have given birth in the same den in which they were born. Females in new prides have less access to such areas even though they settle nearby.

The reasons for the higher mortality of dispersing females in Ngorongoro are difficult to deduce. The most common known cause of female mortality in Ngorongoro is from attacks by Cape buffalo (*Syncerus caffer*) (PACKER, 1986), and perhaps dispersing females are forced to occupy areas without safe refuges from buffalo (*e.g.* trees, see MAKACHA & SCHALLER, 1969). However, adult mortality is generally higher in Ngorongoro than in the Serengeti and this could also be due to higher levels of intraspecific aggression resulting from the higher population density in the Crater (PACKER *et al.*, in press). It seems likely that new prides are subject to considerable aggression from neighboring prides when they first attempt to establish a new range and they might be subject to less harassment from their relatives than they would be from unrelated neighbors (HAMILTON, 1964). This possibility is the subject of current research.

Since dispersing females suffer costs, why do they ever disperse? There are at least three reasons for female dispersal. First, dispersal is often clearly involuntary. Females that are too young to conceive may be evicted at male takeovers (HANBY & BYGOTT, in press, Table 1) and they also tend to leave when their mothers have new cubs, perhaps because of increased aggression. However, females are sometimes able to resist permanent dispersal in both these situations. Second, females often avoid mating with their fathers. Several sets of young females were observed to leave temporarily and to mate with nomadic males, and in one case they left permanently. Female dispersal resulting from females avoiding their close male relatives also appears to occur in several other species (*e.g.* dwarf mongooses (*Helogale parvula*) (ROOD, in press), prairie dogs (*Cynomus ludovicianus*) (HOOGLAND, 1982), horses (*Equus caballus*) (BERGER, 1986), gorillas (*Gorilla gorilla beringei*) (STEWART & HARCOURT, 1987), and chimpanzees (*Pan troglodytes schweinfurthii*) (PUSEY, 1980).

Third, females in excessively large prides have significantly lower reproductive success than those in prides of 3-10 adult females (PACKER *et al.*, in press), so large cohorts might benefit by leaving in spite of the costs of dispersal if their natal pride would otherwise have become greater than 10. Cohorts within the optimum range of pride sizes (3-10) are much more likely to disperse if their natal pride would have exceeded 10 females had they remained. BERTRAM (1973) first suggested that females were more likely to leave their natal pride when pride size was very large and that the size of prides was thus "regulated".

However, many cohorts of 1-2 females left even though their natal pride would have been less than 10 had they stayed. These females are thus subject to the twofold costs of dispersing and of being in too small a pride. It is striking that small cohorts always remain if their natal pride would have become less than three upon the departure of the cohort (Table 3). These results suggest that small cohorts are less able to resist eviction than large ones (since they often leave in spite of higher costs), except in cases where the mothers' group size is also small and then the mothers assist their daughters in staying. In the latter case it is in the mothers' direct interest for their daughters to remain.

Although the dispersal of pairs or single females is common (Table 3) and females in prides of less than three females suffer reduced reproductive success, these small cohorts have not yet been seen to join up with other solitaries (PACKER, 1986). In contrast, solitary males often join up with unrelated companions, but such males often move over large areas before they find unrelated companions and males will move large distances in search of mates (Table 5). The reproductive success of males depends on their ability to gain control of female prides in competition with other male coalitions (BYGOTT *et al.*, 1979; PACKER *et al.*, in press). In contrast, the reproductive success of females may depend critically on familiarity with an area or with neighbors (see above) and thus any advantage from finding an unrelated partner may be outweighed by the costs of dispersing to a new range. Therefore the tendency for females to associate only with kin may in fact result from the strong advantages of natal philopatry.

Two situations are known from other parts of Africa in which unrelated females formed new prides. Following the extensive cropping of lions in portions of Kruger Park, several new prides were formed by females that apparently immigrated into these areas from different prides (SMUTS, 1978). Second, following a severe drought in the Kalahari in which all females abandoned their usual ranges and moved to new areas, females from different prides were observed to join up (OWENS & OWENS, 1984). In both cases it seemed that once females had given up their natal ranges, they readily accepted unrelated companions. We have seen two different pairs of solitary females in temporary and apparently amicable association outside their usual ranges, but they later returned separately to their respective ranges.

These findings are relevant to recent discussions of whether animals ever live in optimally sized groups. Most models predict that groups will typically exceed the optimal size where animals can freely move from group to group (SIBLEY, 1983; PULLIAM & CARACO, 1984). Clearly, lion pride sizes can not conform to predictions based on an ideal free distribution since females associate almost exclusively with kin and many females are forcibly evicted from their natal pride. Under these conditions it is not surprising that the distribution of pride sizes coincides with the optimal range and that there is a slight excess of prides that are smaller than the optimum size (Fig. 3).

When lion prides divide, the division appears to have no consistent effect upon the coefficients of relatedness among females in the resultant prides. This is in contrast to some primate species, where troop fissions are along matrilinial kin lines with the result that average coefficients of relatedness are higher in each new troop than in the original troop (CHEPKO-SADE & SADE, 1979). In lions, any advantages of exclusive association with close kin are often over-ridden by the effects of male takeovers, or recent demographic events such as the birth of cubs.

Male dispersal.

Costs of dispersal.

Male mortality is higher than female mortality at the age of male dispersal. Males of this age are frequently seen with wounds inflicted by other lions, but it is impossible to determine whether mortality from intraspecific competition is higher in dispersing males than it would have been if the males had not left their natal range. Once males have reached the stage that they can successfully take over a pride, costs of dispersal seem to be low because mortality rates do not increase in the month when males first take over a new pride. In general it seems that dispersal might be less costly to males than females since the range of a male coalition depends on the ranges of the prides in which they are resident. The females do most of the hunting (SCHALLER, 1972) and rear their cubs with little direct help from the males. Thus the males need only be able to locate the females to utilize the range efficiently.

Male-male competition.

Intrasexual competition is manifested in a different way in males than in females. Males evict other males from any pride they can whereas females attempt to retain access to a specific area. Consequently most subadult males are evicted from their natal pride by incoming coalitions. Although male-male competition clearly plays a major role in producing male-biased natal dispersal, more males disperse from their natal pride than would be predicted from male-male competition alone. The distance dispersed by males depends on the size and hence competitive ability of their cohort. If a large cohort remains intact it has a shorter nomadic phase and typically becomes resident in a pride adjacent to the natal pride whereas smaller cohorts disperse much further. This is presumably because larger cohorts are better able to evict the resident males of the first few prides they encounter. However, large cohorts were significantly more likely to emigrate from their natal pride than expected from the number of cases in which they were competitively superior to the resident coalition in that pride.

Although the per capita reproductive success of males increases linearly with coalition size it is striking that very large coalitions are so rare. The excess of small coalitions occurs for two reasons. First, only singletons and pairs will enlarge their coalition by joining up with unrelated partners. Therefore, initial coalitions of three or more will never grow larger. Second, large cohorts of subadult males frequently fragment once they have left their natal pride. Some cohorts fragment during their eviction by incoming males but all reunite at least briefly. It may be that remaining together in large groups during dispersal is extremely difficult because of their feeding requirements and because they are frequently harassed by resident prides as they move through their territories. The difficulties of remaining together as nomads might also explain why coalitions of unrelated males do not grow larger than three despite the fact that larger coalitions do better (also see PACKER *et al.*, in press).

We do not yet know the criteria by which small male coalitions select unrelated companions, but we have seen several such males with a variety of companions before a stable coalition was formed. We thus suspect that they actively choose particular partners, and it is possible that the process of finding and choosing an acceptable partner may contribute to the length of their nomadic phase. Alternatively, any male coalition might be willing to acquire an additional partner but will only do so during their nomadic phase (see PACKER & PUSEY, 1983a); and only small coalitions remain nomadic sufficiently long to find an acceptable partner.

Mate acquisition and mate desertion.

Males clearly benefit from moving into new ranges: in 25 cases coalitions of breeding males successfully annexed new prides without surrendering their previous pride. Given the nature of parental care in lions, males gain more from finding additional females than *vice versa* and so male-biased dispersal is not surprising.

However, movements of males between prides often involve risks to their offspring since they thereby expose their cubs to infanticide. Cubs are most vulnerable to infanticide in the first few months of life and males show greater tendencies to remain in prides with such vulnerable young. Males that control several prides simultaneously often surrender one of their prides when they approach the end of their reproductive lifespan. In such cases the result of their movements is that they spend more time with prides containing younger cubs and hence those cubs that benefit most from the males' protection. It thus seems that aging males focus their terminal reproductive effort on existing young rather than attempt to inseminate further females.

Although much of the breeding dispersal of males is explicable in terms of acquiring further mates or protecting existing young, there is also evidence that a third factor is involved in the secondary dispersal of males. Our model for specifying the conditions when males should be willing to abandon existing young in order to gain further females worked well when the cubs in the pride were still small, but males appear to be "too willing" to abandon a pride when their daughters are approaching maturity. Although we clearly need more data to test the robustness of the curve generated in Fig. 8, it is suggestive that males might sometimes move on to avoid their daughters.

In summary, three factors seem to promote secondary emigration of males: gaining access to more females, abandoning older cubs in favor of more vulnerable cubs, and avoiding maturing daughters.

Inbreeding avoidance.

Although inbreeding avoidance may appear to play a relatively minor role in the dispersal of male lions compared to male-male competition or mate acquisition, it does seem to act together with these other factors to make male dispersal ubiquitous. Inbreeding avoidance is implicated in the following aspects of male dispersal. First, males show a tendency to leave their natal pride even when they could presumably have stayed. In the only case where a large cohort bred in their natal pride they moved to the least familiar subgroup of the pride containing no close female relatives. This exception is similar to the only cases of natal breeding by male olive baboons where males either bred with unfamiliar females or with their distant female relatives (PACKER, 1979, 1985).

Second, as in many other species (PUSEY & PACKER, 1987; RALLS *et al.*, 1986), males usually show little interest in mating with females of their natal pride (HANBY & BYGOTT, in press), and even cohorts that join their fathers' coalition do not breed until after departing from their natal pride. Third, although large coalitions may reside in several prides over their lifetimes, return to the natal pride is very rare. This is also the case in social primates (PUSEY & PACKER, 1987). Fourth, males seldom remain and breed in a pride after their daughters have reached sexual maturity and may even move to prides containing considerably fewer females rather than remain and mate with their daughters. A similar tendency for males to leave areas where they have maturing daughters without necessarily gaining access to more females has been found in ground squirrels (*Spermophilus beldingi*) (SHERMAN, 1976, cited in DOBSON & JONES, 1985) and prairie dogs (HOOGLAND, 1982). Finally, it is striking that the only male coalition that bred in their natal group containing familiar females, and the male coalition that remained longest in prides after their daughters had matured were both in the Crater where the choice of prides was severely limited, and the chances of easily taking over a pride outside the Crater were probably low. In other studies, the incidence of close inbreeding is also highest in isolated populations (see RALLS *et al.*, 1986).

Although close inbreeding appears to have detrimental effects on the reproductive physiology of male lions we have little evidence that it confers significant costs on the progeny of incestuous mating partners (Section III). However, inbreeding depression may be only part of the costs of habitual close inbreeding in a large mammalian species. As genetic diversity is lost individuals may be at greater risk from pathogenic infection that becomes adapted to a specific genotype (*e.g.* cheetah (*Acinonyx jubatus*), O'BRIEN *et al.*, 1985). In species of large size and long generation time such as lions the problem of host-parasite coevolution may be particularly acute (HAMILTON, 1980). Although it is possible that the *Stomoxys* plague was solely due to environmental circumstances it is at least worth noting that the inbred Crater population was remarkably susceptible to the effects of the fly. Unfortunately, if increased susceptibility to disease is an important deleterious consequence of higher levels of inbreeding, it will be extremely difficult to measure this quantitatively in naturalistic field studies.

In lions a non-genetic cost of breeding in the natal pride results from the pervasiveness of infanticide as a male reproductive strategy. If there are small cubs present when they take over their natal pride, males must either incur the cost of killing cubs that are their relatives or suffer from an average delay of 8 months before the females are ready to breed again (PACKER & PUSEY, 1984). Such a delay is significant to the males since their average tenure length is only 26 months. Although more data are needed to confirm the generality of this phenomenon, it is striking that in both cases where males bred in their natal group they did not kill the cubs, and thus suffered a delay in breeding. These are the only known cases where incoming males did not kill cubs in the pride. Note, however, that in most of the cases of apparently voluntary natal dispersal, males left even though they would not have been confronted with the prospect of killing their mothers' cubs.

Summary

Most female lions remain in their natal pride for their entire lives, but about a third emigrate before they reach four yrs of age. Most emigrating females leave either when they are evicted by an incoming male coalition or when the adult females of their pride give birth to new cubs. One cohort of females left because they avoided mating with

males of their father's coalition. Cohorts of dispersing females leave together and form a new pride whose range almost always includes at least part of their natal range. Females that leave their natal pride suffer reduced fitness: dispersing females in the Serengeti first breed at a later age than non-dispersing females and dispersing Ngorongoro females suffer higher mortality. Dispersal patterns of large and small cohorts are such that pride size rarely exceeds or goes below the range of sizes that confers the maximum reproductive success per female. Pride fissions have no consistent effect on the average levels of genetic relatedness within prides.

All males leave their natal pride. Most leave at a male takeover, but one male cohort was evicted by their fathers whereas several others left voluntarily during their fathers' tenure. A greater number of large male cohorts leave their natal pride than expected from their competitive ability and males rarely show an interest in mating until they enter a new pride. Larger male coalitions are more likely than small ones to gain residence in a pride adjacent to their natal pride, and also gain their first pride at a younger age. However, not all large cohorts are so successful because most cohorts of 6-8 males permanently split up soon after emigrating from their natal pride.

About half of the secondary dispersal shown by resident adult coalitions is voluntary. Such voluntary secondary movements occur in three contexts: the coalition (1) annexes an additional pride thereby gaining access to more females (2) abandons one of several simultaneously held prides to spend more time with prides in which their cubs are younger and hence more vulnerable to infanticide (3) abandons one pride for another pride. In the third case males only abandon small cubs when going to much larger numbers of females, but they may abandon more females for fewer when their daughters are reaching maturity in the former pride. Males rarely reside in prides once their daughters have matured, and rarely return to breed in their natal pride.

Compared to the large Serengeti population, the small isolated Ngorongoro population has lower levels of dispersal, higher levels of homozygosity and some deleterious effects of inbreeding.

References

BERGER, J. (1986). Wild horses of the Great Basin. — University of Chicago Press, Chicago.

BERTRAM, B. C. R. (1973). Lion population regulation. — E. Afr. Wildl. J. 11, p. 215-225.

—— (1975). Social factors influencing reproduction in wild lions. — J. Zool. 177, p. 463-482.

BRADBURY, J. W. & VEHRENCAMP, S. L. (1977). Social organization and foraging in emballonurid bats. III. Mating systems. — Behav. Ecol. Sociobiol. 2, p. 1-17.

BYGOTT, J. D., BERTRAM, B. C. R. & HANBY, J. P. (1979). Male lions in large coalitions gain reproductive advantages. — Nature 282, p. 838-840.

CHEPKO-SADE, B. D. & SADE, D. S. (1979). Patterns of group splitting within matrilineal kinship groups. — Behav. Ecol. Sociobiol. 5, p. 67-86.

CLUTTON-BROCK, T. H. & HARVEY, P. H. (1976). Evolutionary rules and primate societies. — In: Growing points in ethology (P. P. G. BATESON & R. A. HINDE, eds), p. 195-237. Cambridge University Press, Cambridge.

—— & —— (1984). Comparative approaches to investigating adaptation. — In: Behavioural ecology: An evolutionary approach (J. R. KREBS & N. B. DAVIES, eds), p. 7-29.Sinauer, Sunderland, Massachusetts.

COCKBURN, A., SCOTT, M. & SCOTTS, D. J. (1985). Inbreeding avoidance and male-biased natal dispersal in *Antechinus* spp. (Marsupialia: Dasyuridae). — Anim. Behav. 33, p. 908-915.

CROCKETT, C. M. (1984). Emigration of female red howler monkeys and the case for female competition. — In: Female primates: Studies by women primatologists (M. SMALL, ed.), p. 159-173. Alan R. Liss, New York.

DOBSON, F. S. (1982). Competition for mates and predominant juvenile male dispersal in mammals. — Anim. Behav. 30, p. 1183-1192.

—— & JONES, W. T. (1985). Multiple causes of dispersal. — Am. Nat. 126, p. 855-858.

ELLIOTT, J. P. & COWAN, I. McT. (1978). Territoriality, density, and prey of the lion in Ngorongoro Crater, Tanzania. — Can. J. Zool. 56, p. 1726-1734.

FOSBROOKE, H. (1963). The *Stomoxys* plague in Ngorongoro, 1962. — E. Afr. Wildl. J. 1, p. 124-126.

GREENWOOD, P. J. (1980). Mating systems, philopatry and dispersal in birds and mammals. — Anim. Behav. 28, p. 1140-1162.

——, HARVEY, P. H. & PERRINS, C. M. (1978). Inbreeding and dispersal in the great tit. — Nature (Lond.) 271, p. 52-54.

HAMILTON, W. D. (1964). The genetical evolution of social behavior, I & II. — J. theor. Biol. 7, p. 1-52.

—— (1980). Sex *versus* non-sex *versus* parasite. — Oikos 35, p. 282-290.

HANBY, J. P. & BYGOTT, J. D. (1979). Population changes in lions and other predators. — In: Serengeti: Dynamics of an ecosystem (A. R. E. SINCLAIR & M. NORTON-GRIFFITHS, eds), p. 249-262. University of Chicago Press, Chicago.

—— & BYGOTT, J. D. (in press). Why do subadult lions leave their natal pride? — Anim. Behav.

HAUSFATER, G. & HRDY, S. B. (eds) (1984). Infanticide: Comparative and evolutionary perspectives. — Aldine, New York.

HOOGLAND, J. L. (1982). Prairie dogs avoid extreme inbreeding. — Science 215, p. 1639-1641.

ITANI, J. (1972). A preliminary essay on the relationship between social organization and incest avoidance in non-human primates. — In: Primate socialization (F. E. POIRIER, ed.), p. 165-171. Random House, New York.

JARMAN, P. J. (1974). The social organisation of antelope in relation to their ecology. — Behaviour 48, p. 215-267.

KRUUK, H. (1972). The spotted hyena. — University of Chicago Press, Chicago.

LIBERG, O. & SCHANTZ, T. VON (1985). Sex-biased philopatry and dispersal in birds and mammals: the oedipus hypothesis. — Am. Nat. 126, p. 129-135.

MAKACHA, S. & SCHALLER, G. B. (1969). Observations of lions in Lake Manyara National Park, Tanzania. — E. Afr. Wildl. J. 7, p. 99-103.

MAYNARD SMITH, J. (1977). Parental investment: A prospective analysis. — Anim. Behav. 25, p. 1-9.

MOORE, J. & ALI, R. (1984). Are dispersal and inbreeding avoidance related? — Anim. Behav. 32, p. 94-112.

O'BRIEN, S. J., ROELKE, M. E., MARKER, L., NEWMAN, A., WINKLER, C. A., MELTZER, D., COLLY, L., EVERMANN, J. F., BUSH, M. & BUSH, D. E. (1985). Genetic basis for species vulnerability in the cheetah. — Science 227, p. 1428-1434.

ORSDOL, K. G. VAN (1981). Lion predation in Rwenzori national Park, Uganda. — Ph.D. Thesis, Cambridge.

OWENS, M. & OWENS, D. D. (1984). Kalahari lions break the rules. — Int. Wildl. 14, p. 4-13.

PACKER, C. (1979). Inter-troop transfer and inbreeding avoidance in *Papio anubis*. — Anim. Behav. 27, p. 1-36.

—— (1985). Dispersal and inbreeding avoidance. — Anim. Behav. 33, p. 666-668.

—— (1986). The ecology of sociality in felids. — In: Ecological aspects of social evolution (D. I. RUBENSTEIN & R. W. WRANGHAM, eds), p. 429-451. Princeton Press, Princeton.

——, Herbst, L., Pusey, A. E., Bygott, J. D., Hanby, J. P., Cairns, S. J. & Borgerhoff-Mulder, M. (in press). Reproductive success of lions. — In: Reproductive success (T. H. Clutton-Brock, ed.), University of Chicago Press, Chicago.

—— & Pusey, A. E. (1982). Cooperation and competition within coalitions of male lions: kin selection or game theory? — Nature 296, p. 740-742.

—— & —— (1983a). Cooperation and competition in lions. — Nature 302, p. 356.

—— & —— (1983b). Male takeovers and female reproductive parameters: a simulation of oestrus synchrony in lions (*Panthera leo*). — Anim. Behav. 31, p. 334-340.

—— & —— (1983c). Adaptations of female lions to infanticide by incoming males. — Am. Nat. 121, p. 716-728.

—— & —— (1984). Infanticide in carnivores. — In: Infanticide: Comparative and evolutionary perspectives (G. Hausfater & S. B. Hrdy, eds), p. 31-42. Aldine, Hawthorne, NY.

Pennycuick, C. & Rudnai, J. (1970). A method of identifying individual lions, *Panthera leo*, with an analysis of the reliability of the identification. — J. Zool. 160, p. 497-508.

Pulliam, H. R. & Caraco, T. (1984). Living in groups: is there an optimal group size? — In: Behavioural ecology: An evolutionary approach (J. R. Krebs & N. B. Davies, eds), p. 122-147. Sinuaer, Sunderland, Mass.

Pusey, A. E. (1980). Inbreeding avoidance in chimpanzees. Anim. Behav. 28, p. 543-552.

—— & Packer, C. (1987). Dispersal and philopatry. — In: Primate societies (B. B. Smuts, D. L. Cheney, R. M. Seyfarth, T. Struhsaker & R. W. Wrangham, eds), p. 250-266. University of Chicago Press, Chicago.

Ralls, K., Harvey, P. H. & Lyles, A. M. (1986). Inbreeding in natural populations of birds and mammals. — In: Conservation biology (M. Soule, ed.), p. 35-56. Sinauer, Sunderland, Mass.

Rood, J. P. (in press). Dispersal and intergroup transfer in the dwarf mongoose. — In: Patterns of dispersal among mammals and their effects on the genetic structure of populations (D. Chepko-Sade & Z. Halpin, eds). University of Chicago Press, Chicago.

Rogers, L. C. (1977). Social relationships, movements, and population dynamics of black bears in Northeastern Minnesota. — Ph.D. Thesis, Univ. of Minnesota.

Rudnai, J. (1974). The social life of the lion. — Medical & Technical Publishing, St. Leonardsgate, England.

Schaller, G. B. (1972). The Serengeti lion. — University of Chicago Press, Chicago.

Sibley, R. M. (1983). Optimal group size is unstable. — Anim. Behav. 31, p. 947-948.

Smuts, G. L. (1978). Responses of free-ranging lions (*Panthera leo*) to experimental cropping operations. — Carnivore 1, p. 61-72.

——, Hanks, J. & Whyte, I. J. (1978). Reproduction and social organization of lions from the Kruger National Park. — Carnivore 1, p. 17-28.

Stewart, K. J. & Harcourt, A. H. (1987). Gorillas. — In: Primate societies (B. B. Smuts, D. L. Cheney, R. M. Seyfarth, T. Struhsaker & R. W. Wrangham, eds), p. 155-164. University of Chicago Press, Chicago.

Trivers, R. L. (1972). Parental investment and sexual selection. — In: Sexual selection and the descent of man (B. Campbell, ed.), p. 136-179. Aldine, Chicago.

Waser, P. M. (1985). Does competition drive dispersal? — Ecology 66, p. 1170-1175.

—— & Jones, W. T. (1983). Natal philopatry among solitary mammals. — Q. Rev. Biol. 58, p. 355-390.

Wildt, D. E., O'Brien, S. J., Packer, C., Brown, J. L. & Bush, M. (1986). Reproductive and genetic consequences of founding an isolated population of East African lions. — Abstr. Soc. Stud. Reprod.

Wrangham, R. W. (1980). An ecological model of female-bonded primate groups. — Behaviour 75, p. 262-300.

Appendix 1

Calculating the number of females that must be gained when a new pride is taken over to offset the loss of cubs of various ages in the abandoned pride.

When males have cubs of age x in a pride their expected payoff from remaining in the pride is:

$$n_1(V_x(1-p_x) + q_xV_o)$$

where n_1 = the number of females in the pride that had produced those cubs (most females give birth synchronously in the first few months after a takeover).

V_x = the reproductive value of cubs at age x.

p_x = mortality of cubs of age x when exposed to a takeover; hence, $V_x(1-p_x)$ is the gain in reproductive value of the cohort of cubs if the fathers remain (data from Fig. 6; where non-infanticidal mortality has been removed and the data smoothed to fit a sigmoidal function).

q_x = the proportion of mothers of the first cohort that have resumed breeding x mos after the birth of that cohort (the median interbirth interval is 730.5 days, range 338-939 days, n = 38 females whose first cubs survived; gestation is 110 days, and thus females resume breeding 228-829 days after giving birth).

V_o = the reproductive value of cubs at conception = reproductive value at birth (data from Packer *et al.*, in press; data on age specific survival excludes deaths caused by male takeovers).

The payoff from entering a new pride is:

$$rn_2V_o$$

where n_2 = the number of females in the new pride that conceive.

r = proportion of males that survive the extra three months required by females to conceive when mating with unfamiliar males after a takeover (see Packer & Pusey, 1983b). r is calculated from the mortality rates of males 5-8 yrs old (the age range of males that showed such movements) given in Packer *et al.*, in press.

Thus males will do better to give up on one breeding effort in order to initiate a new one only when:

$$rn_2V_o > n_1(V_x(1-p_x) + q_xV_o), \text{ or when:}$$
$$n_2/n_1 > [V_x(1-p_x) + q_xV_o]/rV_o.$$

This model assumes that there is no significant difference in cub survival between the first cubs born after a takeover (Serengeti: 45% survive to 12 mos of age; Ngorongoro: 60%) compared to cubs of females whose previous litter survived (Serengeti: 41%, Ngorongoro: 56%). It also assumes that there are no costs of moving from one pride to another (see Section II C) and that the previous pride is taken over in the same month that the fathers abandon it. We have also ignored the increasing reproductive value of subsequent litters in the first pride and thus the expected values of n_2/n_1 in Fig. 8 for cubs aged more than about 16 mos are somewhat too low.

Note that the gain in number of females must be fairly high until the cubs in the first pride are about 8 mos old; thereafter, their chances of survival without their fathers' protection are sufficiently high (and the number of mothers who are ready to resume mating sufficiently low) that it would pay males to move into smaller prides. As the number of females that resume breeding increases, then the coalition should only be willing to move on to a larger pride since they can mate with most of the females in the previous pride and can continue to protect their first batch of cubs.