REPRODUCTIVE SUCCESS

Studies of Individual Variation in Contrasting Breeding Systems

Edited by T.H. Clutton-Brock

23 Reproductive Success of Lions

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A FRICAN LIONS FACE FUNDAMENTALLY different eco-
logical problems than most other mammals do, and
they also depend more on cooperative behavior than virtually any other
vertebrate. Lions are territorial but prey primarily upon large herbivores
that are often migratory (Schaller 1972). Thus in some habitats the lions'
food supply is highly erratic and ephemeral, whereas in others it is more
stable. Lions resemble other social carnivores and many higher primates
in being long-lived and highly social. However, they differ in that they do
not typically form dominance hierarchies (Schaller 1972; Bertram 1978;
Bygott, Bertram, and Hanby 1979; Packer and Pusey 1982, 1985). The lack
of social dominance is perhaps an essential feature of lion sociality,
because each individual may therefore be equally affected by any factor
that raises or lowers the reproductive success of the entire group (ibid.;
also see Caraco and Wolf 1975; Vehrencamp 1983). In this chapter we
examine the major ecological and social factors influencing reproductive
success in lions, with special reference to the effects of group size. We
contrast populations living in three widely differing habitats and confirm
that both sexes derive inherent advantages from living in groups.

23.1 Methods

Long-term records are maintained on all the lions in Ngorongoro Crater
and in a 2,000 km² area of the Serengeti National Park, Tanzania (fig.
23.1). The Serengeti study area includes two distinct habitats: the eastern
plains and the woodlands around Seronera. All the lions in these areas
have been studied continuously since 1974 or 1975 (Hanby and Bygott
1979; Packer and Pusey 1982), and two of the woodlands prides have been
studied since 1966 (Schaller 1972; Bertram 1975). These areas typically
contain a total of about three hundred individuals residing in fifteen to
twenty social groups ("prides").

A *pride* is a fission/fusion social unit of one to eighteen adult females
and their dependent offspring. Membership in the pride is stable, but pride

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females are usually in smaller subgroups scattered throughout the pride range (Schaller 1972; Packer 1986). All females of the same pride are genetic relatives in our study areas: females either join their mothers' prides or form new ones with members of their natal cohort (Pusey and Packer 1987). All females in the same pride breed at a similar rate (Schaller 1972; Bertram 1975; Packer and Pusey 1983b). A *coalition* of one to seven adult males maintains residence in the pride for about two years before being replaced by another coalition (Bygott, Bertram, and Hanby 1979; Packer and Pusey 1982). Both females and males are considered adult at four years. Four is the median age when females have their first surviving litter (see below) and the median age when males first become resident in a pride (Pusey and Packer 1987).

All lions resident in the study areas are individually recognizable from
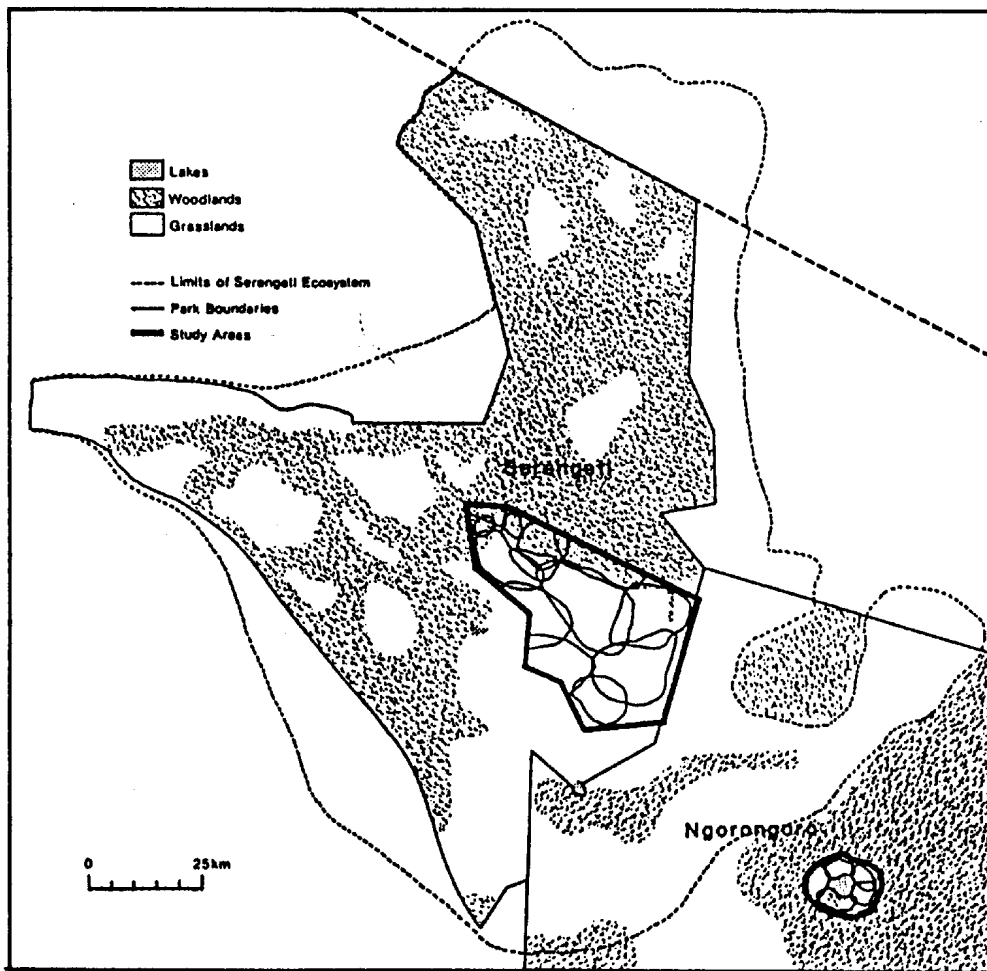
Figure 23.1: Study areas in Serengeti National Park and Ngorongoro Conservation Area, Tanzania. Approximate pride ranges are drawn in the study areas. The woodlands prides are those whose ranges are primarily in the woodlands habitat at the northern edge of the study area.

natural markings (see Pennycuick and Rudnai 1970), and we also identify all nomadic lions that enter the areas. We attempt to locate every resident at least once every two months and to record their reproductive condition (see Packer and Pusey 1983b). Birth dates of cubs can be estimated, but initial litter size can never be known with certainty, since females hide their cubs until they are four to six weeks old. Estimated litter size is one to six, and 98% of litters are one to four (Packer and Pusey 1987). Litters that are lost before the cubs are seen are assumed to have consisted of only one cub, because females often abandon single cubs (Rudnai 1973; Packer and Pusey 1984). Cubs that disappear before the age of eighteen months are assumed to have died, unless their mothers disappeared at the same time and were believed to have emigrated. Older individuals are assumed to have died if they disappear singly; if two or more individuals disappear simultaneously, it usually indicates emigration (see Pusey and Packer 1987).

Demographic data in this chapter come from the authors' observations and from data given in Bertram (1975). In spite of the continuity of these studies, there have been numerous gaps of over six months in observations of each pride, and thus certain data have not been collected with precision. Females may have given birth unnoticed if the entire litter died at an early age, and males may have briefly become resident unnoticed. We have not interpolated birthrates of females during these gaps, but no gap was long enough for us to miss cubs that reached one year of age (our primary measure of reproductive success).

If females of the same pride give birth synchronously, they typically pool their cubs and rear them communally. If "communal litters" are formed during gaps in observations, then we cannot assess maternity. In these cases we award each mother an equal proportion of the communal litter, since females often do have equal numbers of cubs in such litters and certainly do have more cubs than females that did not contribute to it. About 70% of the 1,237 cubs born during the study could be attributed to specific mothers, 15% to a pair of females, and the remainder to three to eight females. Thus our estimates of variance in reproductive success between individual females may be slightly low, but only a small proportion of each female's total cubs were in such litters, and thus the bulk of her reproductive success was accurately recorded.

Our data on the lifetime reproductive success of females are based on the performance of fifty-nine females that died after reaching four years of age. This sample was biased toward younger females, and we therefore calculated the expected age distribution at death of a cohort of fifty-nine from the survival data given in figure 23.4. We thus discarded at random fourteen of the females that had died between four and twelve years of age and replaced them with fourteen living females of thirteen to seventeen years. We extrapolated the reproductive success of six of these living females for one to two years and added cubs both according to the age-specific data given in figure 23.3 and according to each individual's deviation from the mean reproductive success for her age.

Data on mating activity by individual males are far too sparse to use as an index of reproductive success within breeding coalitions, and our estimates of male reproductive success make two assumptions. First, we assume that all cubs conceived during a coalition's tenure were fathered by members of that coalition. This cannot be verified until the paternity exclusion analysis currently in progress is completed. However, we have no behavioral data to suggest that nonresident males ever father cubs, except in the rare cases where fathers are still resident when their daughters reach maturity. Females typically avoid mating with their fathers and will temporarily leave their prides to mate with unfamiliar males (see Pusey and Packer 1987). The current analyses remain essentially unchanged if we assume that either all or none of the cubs were conceived by these females' fathers. Second, we assume that coalition partners have equal reproductive success during their lifetimes. This assumption will also be tested by biochemical analysis. However, observations of mating activity and the fact that females often show synchrony in estrus suggest that coalition partners often have comparable reproductive success (Bertram 1975, 1976; Bygott, Bertram, and Hanby 1979; Packer and Pusey 1982, 1983b). A coalition may remain in residence after the death of one or more of its members, and individual reproductive success is therefore calculated by awarding each male an equal proportion of the cubs conceived in his lifetime.

Results are presented separately for each habitat whenever there is no significant concordance between habitats. If trends for each habitat differ in elevation but not in slope for a particular analysis, then pooled data are graphed and the habitat differences noted. In some analyses, statistics have had to be based on the number of cubs that were born or died in particular circumstances. Cubs of the same litter cannot be treated as statistically independent because they are born and often die at the same time. We have therefore divided the number of cubs by two (the approximate average litter size) and calculated chi-square values from the number of "litters." Similarly, except for the analysis of individual reproductive success in table 23.1 and figure 23.2, statistical tests on males are based on average values for each coalition, since coalitions act as a unit.

Annual rates are calculated according to weather year (the beginning of one rainy season until the end of the following dry season—for example, November 1976–October 1977). Because of the effect of rainfall on the movements of the migratory herds in the Serengeti (see below), we have relied on rainfall as an indicator of prey availability. Although nearly thirty rain gauges are ready every month in the Serengeti study area, no good rainfall data are available for the crater floor. However, because the rainfall on the eastern Serengeti plains generally comes from the east, we have used those data to estimate rain in the crater.

23.2 Study Sites

The Ngorongoro Crater is a large volcanic caldera that contains one of the highest lion population densities in Africa (van Orsdol 1981). The crater floor is mostly open grassland but includes a number of swamps and marshes. These wetlands flood during the rainy season (November–May), and thus green grass is continuously available around their edges as the water recedes during the dry season. Although most of the larger ungulates show daily and seasonal movements around the crater floor, only a small proportion of wildebeest and zebra leave the crater in the wet season, and most of the buffalo and eland leave in the dry season (Kruuk 1972; Estes and Estes 1979). Thus there is only minor seasonal variation in the overall herbivore biomass in the crater (van Orsdol 1981), and the resident biomass of the lions' preferred prey species is the highest in Africa.

The crater is surrounded by highland forest around two-thirds of its circumference and by arid scrub/grasslands occupied by Masai tribesmen around the remaining third. Resident lion prides occasionally move up the crater walls, and there is evidence that a considerable proportion of subadults permanently emigrate from the crater (Pusey and Packer 1987). However, the surrounding area appears to support a far lower lion density than the crater floor, and no immigration into the crater has been recorded in the past ten years. Thus the crater is essentially a self-contained ecological unit, and the lions are a distinct and isolated population. The crater lion population crashed in 1962 (Fosbrooke 1963), reached its current level by 1975, and has since been stable (Pusey and Packer 1987).

In contrast, the Serengeti ecosystem is defined by the vast migration of its dominant herbivores (figure 23.1). The wildebeest, zebra, and gazelle all prefer to graze on the eastern plains, where the soil is mineral-rich volcanic ash from the crater highlands to the east (Kreulen 1975). Rainfall is sufficient to stimulate grass growth on the plains only during a few months in each rainy season (November–May; McNaughton 1979), and rainfall levels are lower on the plains than elsewhere in the Serengeti ecosystem (Sinclair 1979). The lion population in the plains thus has access to plentiful prey only during these rainy months. During the dry season, only a few warthog, topi, oryx, and Grant's gazelle remain on the plains (Hanby and Bygott 1979). However, if there is sufficient rainfall during the normally dry months of June–October, wildebeest and zebra will return briefly to the northern and western edges of the plains, and the plains lions temporarily move to the edge of the woodlands when prey is scarce on the plains. Several prides on the Serengeti plains are known to have originated from adjacent areas of woodlands (Hanby and Bygott 1979). The size and number of prides on the plains increased between 1966 and 1976 (Hanby and Bygott 1979), and the number of adult females living on the plains has increased continuously from 1973 to 1984 ($r_s = .846$, $n = 12$ years, $p <$ .01).

The woodlands area around Seronera is both a dry-season refuge for many herbivores and also a "holding area" for the migratory species as

they go to and from the plains. The area is on the migratory route during the changes between seasons and is visited by some of the migratory herds during dry spells in the rainy season and wet spells in the dry season (see Maddock 1979). When the wildebeest and zebra are absent in the dry season, these lions prey primary upon buffalo and gazelle (Packer 1986). Rainfall is heavier here than on the plains at all times of year, but in the wettest part of the rainy season prey may become scarce, and these lions will make temporary forays more than 25 km onto the plains in extremely wet years (Schaller 1972; pers. obs.). The lion population in this area also increased between 1966 and 1974 (Hanby and Bygott 1979), but it has since stabilized.

23.3 Results and Discussion

In the following sections we first compare the lifetime reproductive success (LRS) of females and males and specify the causes of variance in the reproductive success of each sex. We then describe in detail the causes of mortality of cubs and of adults, since these are important determinants of reproductive success. Finally, we show how the reproductive success of both sexes depends on group size.

Lifetime Reproductive Success

"Reproductive success" is defined as the number of offspring reaching twelve months of age. A large proportion of subadults disperse from the study areas between the ages of one and one-half and four years (Pusey and Packer 1987), and thus data on the number of offspring reaching reproductive age are incomplete.

Females

Figure 23.2 shows the frequency distribution of lifetime reproductive success of breeding females. Age-specific measures of female reproduction are given in fig. 23.3. Female lions typically have their first litter at three to four years of age, and their reproductive performance starts to decline at eleven years (fig. 23.3). Data on birthrates and litter size are only approximate (see Methods, above) but data on the number of cubs surviving to twelve months are accurate. These show that female reproductive success also declines at eleven years and virtually stops at fifteen years. Survival of cubs does not change significantly with maternal age. The average interbirth interval for females whose previous cubs survived is twenty-four months (Pusey and Packer 1987), and the peaks in reproductive success at three, five, seven, and ten years presumably reflect this interval.

Tables 23.1–23.3 show the relative importance of life span, fecundity, and cub survival on the lifetime reproductive success of the breeding females that reached eight years of age. We restrict this analysis to females that reached eight years because of the statistical artifact that arises from

excluding nonbreeders from the sample. Variance in fecundity is highest shortly after maturity, since late first breeders have zero fecundity at their death, whereas early first breeders have a high apparent fecundity at death because of the brief duration of their reproductive life span. Consequently there was a significantly negative correlation between life span and fecundity among all *breeders* that reached four years of age ($r_s = -.3346$, $n = 54$, $p < .05$), but not over all females that reached four years ($r_s = -.0538$, $n = 59$, n.s.).

Tables 23.1–23.3 suggest that although all three variables make a substantial contribution to the lifetime reproductive success of breeding
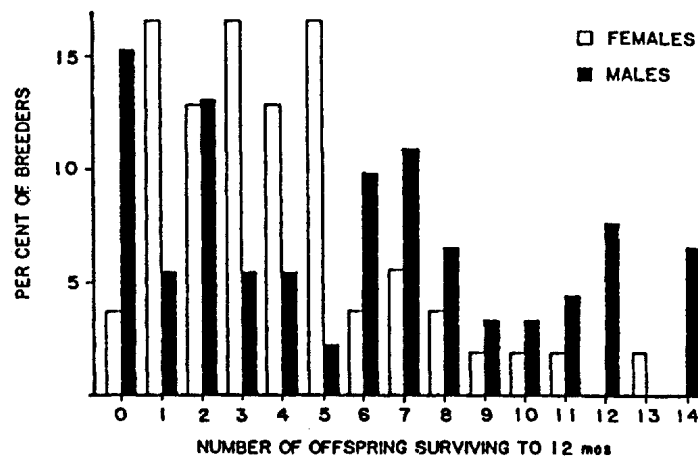

Figure 23.2: Lifetime reproductive success of males and females. Frequencies are given in terms of the percentage of breeders of each sex (males: $n = 91$; females: $n = 54$; see text). Any possible effects from differences across habitats have been ignored.
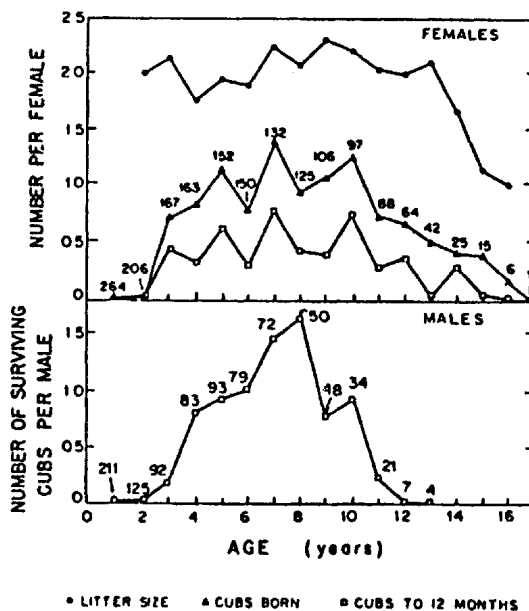

Figure 23.3: (*a*) Age-specific reproduction of females. Numbers above birthrates give sample size for each age. There were no habitat differences in any of these measures. (*b*) Age-specific reproductive success of males. Data include nonbreeding males as well as those that were members of resident coalitions.

Table 23.1 Mean and Variance of the Components of Lifetime Reproductive Success in Lions

Component	Original		Standardized Variance
	Mean	*Variance*	
Females (n = 54)			
L	7.7374	10.3595	0.1730
F	1.2968	0.5299	0.3151
S	0.4374	0.0621	0.3246
LF	9.0035	17.8392	0.1772
FS	0.5474	0.2419	0.7520
LS	3.4400	5.4318	0.4742
LFS	3.8100	7.8029	0.4051
Males (n = 31 coalitions)			
L	4.4731	3.8675	0.1933
F	2.2757	2.7177	0.5247
S	0.3843	0.0725	0.4908
LF	9.3420	48.3257	0.4665
FS	1.1337	1.4939	1.9531
LS	1.7137	2.0331	0.6880
LFS	4.4796	17.1047	1.1175

Source: Program developed by David Brown (see this volume, chap. 27).
L = life span; F = fecundity; S = cub survival.

Table 23.2 Percentage Contribution of the Components of Lifetime Reproductive Success to Variation in LRS in Lions

Component	L	F	S
Females[a]			
L	21.71		
F	−25.17	39.45	
S	−15.05	42.60	84.57
LFS	−48.10		
Males[b]			
L	17.30		
F	−22.51	46.95	
S	0.33	83.88	43.93
LFS	−69.89		

Source: Program developed by David Brown (this volume, chap. 27).
L = life span; F = fecundity; S = cub survival.
[a]Forty-seven breeding females that survived to eight years.
[b]Breeding male coalitions.

Table 23.3 Partition of Lifetime Reproductive Success in Lions: Inclusion of Nonbreeders

	Females (number of breeders = 54)	Individual Males (number of breeders = 91)
Proportion of breeders	0.3293	0.2218
Overall variance (OV)	5.8607	8.7288
Percentage of OV due to nonbreeders	55.74	52.32
Percentage of OV due to breeders	44.26	47.68

Source: Program developed by David Brown (this volume, chap. 27).

females, cub survival is the most important component. However, life span is probably more important than the tables indicate. We have had to include only females over eight years of age, whereas a number of adult females died before that age. When all females that reached four years of age are included, life span accounts for 43% of the variance. We will discuss causes of mortality in both cubs and adults in subsequent sections of this chapter.

The importance of fecundity is difficult to assess. Fecundity should be *inversely* related to cub survival in lions, because females that lose their cubs resume breeding much more quickly than those whose cubs survive (see Packer and Pusey 1984). Thus a female that lost every litter shortly after birth might have a litter once every four to six months (and have a high fecundity), whereas a female that successfully reared each litter would have a litter only once every eighteen to twenty-four months (and have a relatively low fecundity). The positive correlation between survival and fecundity in tables 23.1–23.3 probably results from our inability to detect many litters that die at an early age (see Methods), and thus our data greatly underestimate the fecundity of females with low cub survival. Therefore the apparent relationship between fecundity and reproductive success may not be valid.

Males

Figure 23.2 shows the estimated lifetime reproductive success of ninety-one males that became resident in the study prides. No attempt has been made to correct the age structure of this sample as was done for females (see Methods), because the average reproductive life span of males is only thirty-three months (range 5–130 months, $n = 31$ coalitions). However, these data include a number of males that are still breeding and an unknown number of males that may have been resident outside the study areas before or after they resided in a study pride (see note to table 23.5). Furthermore, we have assumed that there is no variance in reproductive success within coalitions except that due to male mortality (see Methods). Thus these estimates are too low and should be considered rough approximations. We include them in order to compare variance in male reproductive success with that for females and because more complete data would probably not substantially alter the shape of the overall distribution.

As would be expected in a polygynous species, variance is higher in male reproductive success than in that of females (tables 23.1–23.3), and the true magnitude of this difference is probably greater than these data indicate.

Reproductive success is confined to a narrower range of ages in males than in females (fig. 23.3b) Male coalitions must compete successfully against other coalitions in order to gain and retain residence in prides (Schaller 1972; Bertram 1975; Bygott, Bertram, and Hanby 1979). Larger coalitions oust smaller ones from prides and chase nomadic coalitions

SURVIVAL OF FEMALES

SURVIVAL OF MALES
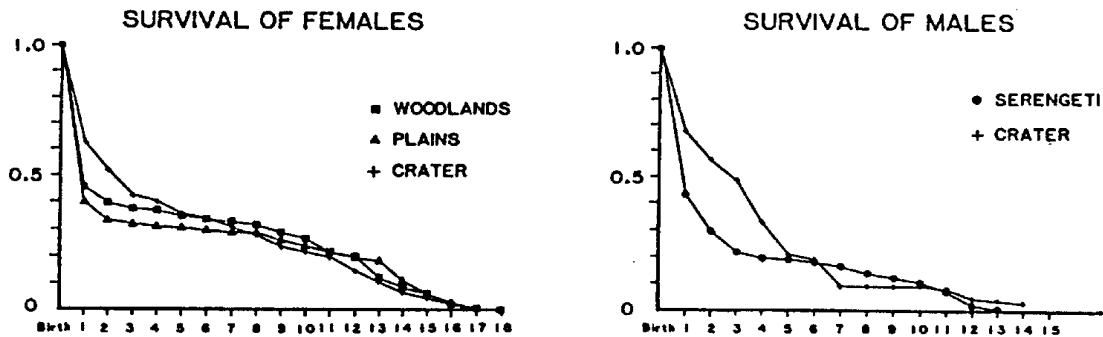
Figure 23.4: Survival curves for each sex in each habitat. Mortality rates from birth to one year of age were significantly higher in the Serengeti plains (1974–84) than in the woodlands (1966–84) (χ^2 = 6.887, n = 426 "litters," p < .01), and mortality in the woodlands was higher than in Ngorongoro Crater (1975–84) (χ^2 = 9.320, n = 412, p < .01). Data include all individuals alive when records were begun in each area and all males that immigrated into the study prides from elsewhere. Initial age estimates of these individuals are made by comparing photographs with those of known-age individuals. Individuals that "disappeared" rather than died (see Methods) were included as survivors for each age before their disappearance. Because males are more likely to disperse from the study areas than females (Pusey and Packer 1987), and because substantial rates of disappearance result in underestimates of mortality, we have corrected for this sex bias by estimating true mortality of males from the sex ratio at each age.

from their prides' ranges. Although such encounters typically involve only chasing, gang attacks also occur, and severe injuries may be inflicted. Thus males must be old enough and healthy enough to compete successfully for residence in a pride.

Successful males become resident in their first pride when they are about four years old (Pusey and Packer 1987), and their first cubs are born about six months later (Packer and Pusey 1983a). Male coalitions remain in individual prides for an average of only twenty-six months, but some large coalitions gain residence in a succession of prides (Pusey and Packer 1987). However, even males in these coalitions look conspicuously old by ten years of age, being covered with scars and wounds, and very few survive to twelve years (see fig. 23.4). After an aging coalition loses residence, the males' small cubs are usually killed by the replacement coalition (see below).

Tables 23.1–23.3 show the relative contributions of life span, fecundity, and cub survival to male lifetime reproductive success. Overall, these components have effects similar to their effects in females, except that cub survival appears somewhat less important to male reproductive success. Fecundity and cub survival are highly correlated, probably because the cubs of males with high "fecundity" were born synchronously to many females shortly after those males took over their pride. Such synchronous litters are subsequently reared communally and have higher survival than cubs born asynchronously (Bertram 1975). It is doubtful that coalitions actually do vary in fecundity; such variation probably results from conditions affecting the females in the prides where they gain residence.

Lifetime reproductive success of males is also significantly correlated with coalition size (r_s = .4110, n = 31 coalitions, p < .05), time spent in residence in prides over their lifetime (overall tenure length) (r_s = .7963, p < .001), and the total number of females in the prides held during their lifetime (r_s = .5819, p < .001). Of these, only coalition size relates directly to differences in competitive ability; the other two are consequences of competitive ability. (Note that these analyses include only coalitions that maintained residence long enough to father cubs; many coalitions never do so; see table 23.5.)

Tenure length is one of the most important components of lifetime reproductive success of breeding males, but tenure is highly correlated with coalition size (r_s = .7372, p < .001). Males that maintain residence long enough are able to protect their young from infanticide by subsequent coalitions (tenure vs. cub survival: r_s = .5797, p < .001). Males that remain in the same pride long enough to sire successive litters also gain from the fact that females conceive three months sooner when mating with males that have sired their previous cubs than when mating with males that have just entered their pride (Packer and Pusey 1983a). Tenure and fecundity are significantly correlated (r_s = .5505, p < .01).

The number of females gained by each coalition is also correlated with coalition size (r_s = .5745, p < .001). This is because larger coalitions gain more prides during their careers (coalition size vs. number of prides held: r_s = .7782, p < .001). They do not preferentially become resident in large prides (coalition size vs. average size of prides held: r_s = .0076, n.s.).

Coalition size in itself is not as highly correlated with reproductive success as are many other variables, because the advantage of belonging to a coalition of a particular size depends on the average coalition size in the population. This varies from year to year, and when no large coalitions are present, smaller coalitions can maintain residence for long periods. Coalitions of four or more males are always composed of members of the same natal cohort (see below). Natal cohort size depends on cub survival within a pride, and cub survival is synchronized over large areas of the park by weather patterns (see next section). Thus the median coalition size in the Serengeti increased from two in the late 1960s to three in the mid-1970s, following a general increase in the lion population, and has since declined again to two (also see Packer and Pusey 1983c).
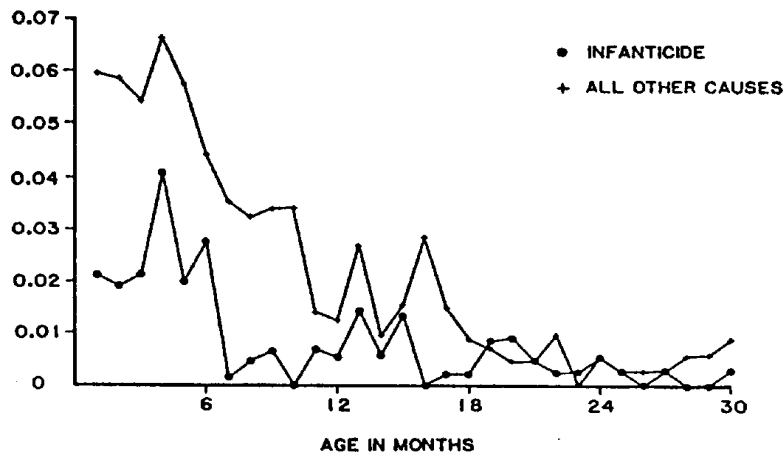
Cub Mortality

Mortality is highest during the first year of life (Schaller 1972; Bertram 1975), and this early mortality varies across habitats: nearly two-thirds of cubs born on the plains die before one year of age, whereas only one-third of crater cubs die by that age (fig. 23.4). Since cubs' deaths are rarely witnessed, it is usually difficult to determine the exact cause. Nevertheless, there are two contexts in which the cause of death can be reliably inferred: male takeovers and season of low prey availability.

Incoming males have been observed to kill unweaned cubs seven

times, and cub mortality rates are much higher in the first months following the arrival of a new set of males than at other times (Bertram 1975; Packer and Pusey 1983a, 1984). Cubs almost never survive more than two months into the tenure of a new male coalition in their mothers' pride. By killing the cubs, males speed up the females' return to sexual receptivity by an average of eight months (Packer and Pusey 1984). All cub mortality within two months of a male takeover is therefore considered here to be due to infanticide. The proportion of deaths attributed to infanticide is similar across all three habitats, and 27% of all mortality before twelve months of age occurs in this context. Infanticide is mostly restricted to cubs of six months or less, though they continue to be at risk until about twenty months (fig. 23.5; also see Pusey and Packer 1987). Cubs older than eighteen months are generally evicted from their natal pride by the new males (Hanby and Bygott 1987; Pusey and Packer 1987).

Schaller (1972) suggested that 50% of cub mortality in the Serengeti was the result of starvation, but though many malnourished cubs have been observed, the death of a starving cub has been seen only once (Packer and Pusey 1984). However, the prevalence of starvation can be inferred from a seasonal pattern of cub mortality that is correlated with seasonality of prey availability. In the Serengeti plains, cub mortality other than that due to male infanticide is highly seasonal: 68% of the remaining cub deaths occur during the dry season, which constitutes only 43% of the year (x^2 = 18.70, 1 d.f., n = 64.5 "litter" deaths [see Methods], $p < .001$). During the dry season, the estimated prey availability on the plains is about one-twenty-fifth that of the rainy season (van Orsdol 1981), and cubs in plains prides are obviously malnourished during dry-season months. In

Figure 23.5: Age-specific mortality owing to infanticide. The overall proportion of deaths that were due to infanticide was similar across all three habitats (Ngorongoro Crater: 22.8%; Serengeti plains: 33.5%; woodlands: 24.9%; x^2 = 2.75, 2 d.f., n.s.), and there was significant concordance in the age at which cubs were most at risk from infanticide (Friedman test: x^2 = 45.26, 30 d.f., $p < .05$), as well as from other causes (x^2 = 62.91, $p < .001$). Sexes are lumped because male and female cubs showed a similar age-related pattern of mortality from infanticide (r_s = .392, n = 30, $p < .05$).

Table 23.4   Correlations between Environmental Conditions in Different Years and Annual Lion Cub Recruitment Rates within Each Habitat

Correlation of Cub Recruitment with	Serengeti Woodlands	Serengeti Plains	Ngorongoro Crater	χ^2	$\hat{p}$	z
Percentage of females exposed to male takeovers	−.4386	−.7341**	−.6273*	0.98	−.6135	3.300***
Dry-season rainfall	.2363	.3614	.3333	0.09	.3105	1.670#
Wet-season rainfall	−.7636**	−.6932*	−.0061	4.59*		
Number of females in habitat	−.3182	−.3386	−.4061	0.05	−.3529	1.898#
Dry-season rain in woodlands	—	.8735***	—			

Note: Data from the Serengeti are for cubs born in 1973–83 (cubs born in 1973 reached one year of age in 1974, the first year of data for most of the study prides). Data from the crater are from 1974–83. When there is no significant heterogeneity in correlations across habitats (given by the χ^2 with 2 d.f.), an overall correlation coefficient ($\hat{p}$) and its associated z value have been calculated (Kraemer 1975).

# $p < .05$, one-tailed test (see text); * $p < .05$, two-tailed test; ** $p < .02$; *** $p < .001$.

contrast, cub mortality is only slightly higher during the dry season in the Serengeti woodlands (49%, $\chi^2 = 2.49$, $n = 110$, n.s.), and there is no indication of seasonality of mortality in Ngorongoro Crater (39%, $\chi^2 = 0.07$, $n = 35.5$, n.s.). In the Serengeti woodlands there are obvious cases of cub starvation in some dry seasons, but this is probably balanced by starvation during the wet season in exceptionally wet years (see below). As outlined above, seasonality of prey availability in this area varies strikingly from year to year. In the crater, we have never seen a conspicuously malnourished cub, and the crater shows virtually no seasonality in prey availability (van Orsdol 1981). Mortality of individuals older than one year does not show significant variation across seasons in any of the three habitats.

Van Orsdol (1981) found that cub survival to twelve months was highly correlated with poor-season biomass across six habitats that included our three sites and that by themselves are in accordance with this trend. This suggests that food availability is a major determinant of cub survival in the most seasonal areas but that other factors must be acting to limit populations in nonseasonal areas.

Schaller (1972) saw cubs being killed by other species of carnivores, and there is also evidence that cubs die owing to accidental maternal neglect and intentional abandonment (Packer and Pusey 1984). However, we have no way of assessing the relative importance of these causes of mortality, since we cannot define a context when such mortality is likely to occur. More extensive observations of death are required.

We have examined the major variables that are likely to affect the annual cub recruitment rates in each of our study areas (table 23.4). These variables are directly related to the two major causes of cub mortality outlined above: infanticide and starvation during the season of lowest prey availability. Cub recruitment rate is the number of cubs reaching one year of age per adult female, and high recruitment rates indicate low cub mortality. Across all three habitats, there is a strong negative relationship

between cub recruitment and male takeover rate (table 23.4), as expected because of infanticide by the incoming males. Cub recruitment is predicted to be positively correlated with dry-season rainfall within each of the three habitats, because such rainfall attracts more herbivores to the lions' ranges (see Study Sites, above). However, the overall trend is only weakly significant (table 23.4).

The relation of cub recruitment on the Serengeti plains to dry-season rainfall in the woodlands is far higher than its relation to rainfall on the plains (table 23.4). The plains prides often move to the edge of the woodlands during the dry season, and thus this area appears to be their critical refuge during harsh conditions. Hanby and Bygott (1979) had attributed the population increase on the plains in the early 1970s to higher dry-season rainfall there. However, dry-season rainfall in the two habitats is positively correlated (r_s = .5941, n = 16 years (1969–84), p < .05), and it is the rainfall in the adjacent woodlands that appears to be critical. The soil on the eastern plains is so friable and the dry-season rainfall there is so slight that the resultant growth of green grass is usually insufficient to attract the migratory herbivores for any appreciable period outside the true rainy season.

Cub recruitment is inversely related to wet-season rainfall in both Serengeti habitats (table 23.4), but probably for different reasons in each. The migratory herds return to the woodlands less frequently in the rainy season during extremely wet years, and even resident prey move out to the plains. We have seen emaciated cubs in the woodlands during periods of heavy rain, and thus the woodlands cubs may be more likely to starve in these years. On the plains, greater numbers of nomadic males are attracted to the area during extremely wet years because the migratory herds are present more persistently, and thus takeover rates in the plains prides are highest in wet years (r_s = .800, n = 11, p < .01). Such nomads pass through the woodlands study area on their way to and from the plains, and thus takeover rates there also tend to be higher in wet years (r_s = .452, n = 11, n.s.). Note that wet-season rainfall is not correlated with dry-season rainfall in either area (woodlands: r_s = −.053; plains: r_s = .021, n = 16 years).

It is also possible that higher rainfall may increase mortality through flooding or disease; but if this were the case, recruitment rates in the crater should also be lowest in the wettest years. Following extremely heavy rainfall in the wet season of 1962, there was a "plague" of bloodsucking *Stomoxys* flies in Ngorongoro Crater that reduced the lion population from seventy-five to six to fifteen (Fosbrooke 1963). However, the population had returned to its former level by 1975 (Pusey and Packer 1987), and subsequently there has been no detectable effect of variation in wet-season rainfall on cub recruitment (table 23.4).

Finally, Bertram (1973) suggested that pride sizes might be density dependent. There is some indication that cub recruitment rates are highest in years when the number of females in a habitat is lowest, although this

effect is small (table 23.4). This correlation is not due to increased frequencies of infanticide: the takeover rate in each habitat does not increase significantly with increasing density of females in that habitat. There may be some effect of higher density on cub starvation, but our data are not adequate to detect it.

Adult Mortality

Females

Although cub mortality is higher in the Serengeti than in Ngorongoro Crater, mortality of females is lower at each age from three to ten years (fig. 23.4). In spotted hyenas, a similar contrast between the two areas was deduced from the differing age structures of the two populations (Kruuk 1972). Kruuk suggested that the Serengeti hyenas were limited by prey availability, which resulted in higher cub mortality. In contrast, the crater hyenas were subject to greater territorial aggression and hence to greater adult mortality because of higher population density. Lion density in the crater is four times the density in the Serengeti plains and twice that in the woodlands. Although our findings in figure 23.4 are in broad agreement with Kruuk's, we have no direct evidence that crater females are more frequently killed by intraspecific aggression. One female in the Serengeti was known to be fatally wounded by other females, whereas the only known cause of mortality in adult females in the crater is injury inflicted by Cape buffalo (n = 4). However, a much larger proportion of subadult females disperse from their natal pride in the crater than in the Serengeti (Hanby and Bygott 1987, Pusey and Packer 1987), and we therefore suspect that females are subject to higher levels of aggression in the crater.

Males

After one to three years of age, mortality of males is higher than that of females, and after five years it appears more similar across habitats (fig. 23.4). Males from the two Serengeti habitats have been combined, since males often move back and forth between the two areas. Although a higher proportion of males survive to one year of age in the crater, mortality from ages two to five is far higher, apparently owing to attacks by adult males. Young males often become nomadic after their second year, but whereas young males in the Serengeti can often move to areas unoccupied by residents and can follow the superabundant migratory prey species, young crater males are in more constant contact with resident prides (see Hanby and Bygott 1987) and are often seen with severe wounds. The similarity of male life expectancy in the two areas after five years may be because levels of adult male/male competition are similar regardless of female density.

Group-Size-Specific Reproductive Success

Lions are the only social cat, and it is therefore of considerable importance to determine whether individuals derive a reproductive advantage from living in groups. We analyze separately the effects of grouping on the reproductive success of each sex.

Males

As described above, male lions form stable coalitions that compete intensely against other coalitions for access to female prides. Bygott, Bertram, and Hanby (1979) first showed that per capita male reproductive success increases with coalition size, and their analysis indicated that larger coalitions do better because they are more likely to gain access to a pride, remain in residence longer, and gain access to more females. These findings are all confirmed by our analyses.

Figure 23.6a shows the precise payoff to individual males from belonging to coalitions of different sizes. This provides more complete information on the lifetime reproductive success of the coalitions included
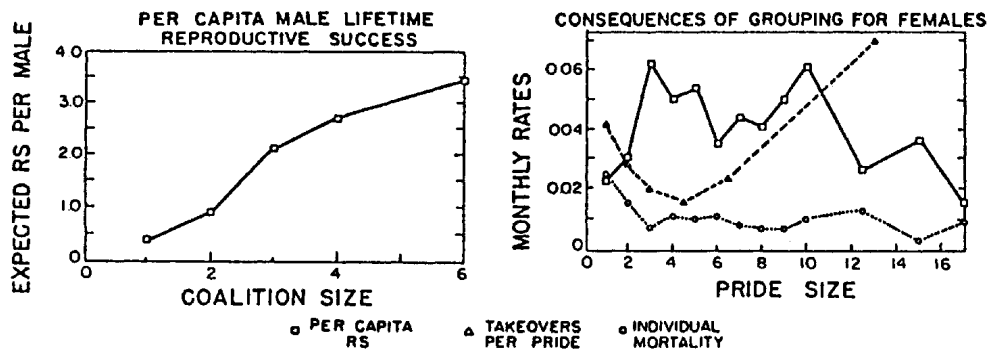
Figure 23.6: (a) Per capita reproductive success versus male coalition size. Calculations are based on data given in table 23.5. There were insufficient data to test for concordance between the Serengeti and the crater, but they showed a similar increase with increasing coalition size. (b) Pride-size-specific reproductive rates, mortality, and frequency of male takeovers. Data from adjacent cells have been combined to provide sufficient sample size in each cell to allow use of chi-square tests. Monthly reproductive rates per female showed significant overall heterogeneity ($\chi^2 = 21.039$, $n = 272.5$ surviving "litters," 12 d.f., $p < .01$). Prides of one or two females had significantly lower reproductive rates than did prides of three to ten ($\chi^2 = 6.585$, $n = 259.5$, 1 d.f., $p < .01$); prides of eleven to eighteen also did worse than those of three to ten ($\chi^2 = 5.250$, $n = 250.5$, $p < .02$). There was no significant heterogeneity among pride sizes of three to ten ($\chi^2 = 8.166$, $n = 237.5$, 7 d.f., n.s.). Mortality of females in prides of one or two females was significantly higher than in larger prides ($\chi^2 = 10.885$, $n = 123$ deaths, 1 d.f., $p < .01$). Heterogeneity across pride sizes in frequency of male takeovers approaches significance ($\chi^2 = 10.48$, $n = 77$ takeovers, 5 d.f., $p < .10$, two-tailed test). Solitary females and those in large prides suffered more frequent takeovers than those in moderate sized prides (solitaries vs. moderate: $\chi^2 = 5.20$, 1 d.f., $p < .05$; large vs. moderate: $\chi^2 = 18.00$, $p < .001$). Although there was a significant difference in per capita reproduction rate between the crater and the plains ($p < .05$), and though the crater females also suffered higher mortality than their Serengeti counterparts (fig. 23.4), there was reasonably high concordance between habitats on the effects of pride size for all three variables.

Table 23.5   Reproductive Success of Male Coalitions in Lions

Coalition Size	Proportion That Stay Together	Proportion That Gain Residence	Average Observed RS per Resident Male (n)	Expected RS per Male
1	—	1/16	6.500 (2)	0.406
2	all	6/14	2.136 (11)	0.915
3	all	6/12	4.249 (12)	2.125
4	all	3/4	3.625 (2)	2.719
5–7	3/8	3/3	9.206 (4)	3.452

Note: Data on the proportion of coalitions remaining together and on those that became resident in prides are restricted to males originating within the study area. Coalitions that fragmented before gaining residence are included in subsequent columns according to their sizes after the split. Males that acquired unrelated companions during thier nomadic phase are included in estimates of the proportion that gain residence according to the size of their coalition both before and after the acquisition. Pairs are significantly more likely to gain residence than are singletons ($p < .05$, Fisher test). Data on per capita reproductive success of resident males include all males regardless of origins but include only the coalitions for which there are data on at least half of their reproductive output. Several other coalitions dispersed into or out of the study areas or only recently gained residence.

in Bygott, Bertram, and Hanby's paper (1979) and includes additional coalitions that became resident after 1977. Per capita reproductive success is estimated by taking the proportion of coalitions of each size that gain exclusive access to a group of females, multiplied by the number of cubs surviving to one year of age that were conceived during the coalition's tenure, divided by the initial number of males in the coalition. Figure 23.6*a* thus gives an estimate of the *expected* reproductive success of each male when the coalition is first formed; some coalition members may die before the remainder have lost tenure (see above). This estimate assumes that coalition partners have equal reproductive success during their lifetimes, and although this may be true in most coalitions (see Methods), males apparently do have disparate success in some (see Packer and Pusey 1982). We discuss the implications of unequal reproductive success below.

Values for each of these group-size-specific factors are listed in table 23.5. It can be seen that the probability of gaining residence increases continuously with increasing coalition size, but the difference is most striking between solitaries and pairs. Per capita reproductive success of resident coalitions also increases with coalition size, but this shows considerable variance (see preceding sections).

Note that we have calculated the proportion of coalitions gaining access to prides in a slightly different way than Bygott, Bertram, and Hanby (1979), who simply divided the number of resident coalitions of each size by the total number of coalitions of that size in the population. We now know that very large coalitions often break up shortly after leaving their natal pride (Pusey and Packer 1987) and thus would not be seen as a large nonresident coalition.

The tendency for solitary males to form coalitions of two to three is expected from the large mutual advantage of cooperation (Packer and Pusey 1982), and coalitions of unrelated males have reproductive success similar to that of comparably sized coalitions composed entirely of

relatives. However, it is puzzling that unrelated males join only up to a maximum of three: nine of fourteen pairs and trios of known origins include nonrelatives, but all six coalitions of four or more males are composed entirely of relatives ($p < .05$, Fisher test). Although males might continue to gain by acquiring further unrelated partners, the gain beyond three may be too small to compensate for the time lost in seeking further companions. Males acquire unrelated companions only while they are not yet resident, and Pusey and Packer (1987) found that males with unrelated partners gained initial residence at a later age than did cohorts of relatives.

Another possible explanation is that although larger coalitions enjoy higher average reproductive success, the temporal patterning of the availability of estrous females may be such that the males in a coalition of four or more are never all able to mate simultaneously, whereas the males in a pair or trio can often do so. This would lead to inherently higher levels of variance in mating success in the large coalitions. Thus males should join them only either when they could predict that they would have a higher reproductive success from joining or when their companions were their close kin. In the latter case a subordinate might still increase his inclusive fitness by enhancing the reproductive success of his dominant brothers even if he had a lower individual mating success than he would in a smaller coalition.

Females

It is not possible to calculate group-size-specific reproductive success for females in the same way as for males. Whereas a male coalition starts at its largest size and then declines through mortality, female pride size may fluctuate widely over time. For example, since 1966 the Masai pride has split into four separate groups, and the number of adult females in the main pride gradually increased from six to eighteen, then slowly declined to seven. Therefore, rather than estimating the per capita lifetime reproductive success for each pride size (as was done in fig. 23.6a), we found the number of surviving cubs that were born in each pride size each month. The number of cubs born each month in each pride size divided by the number of adult females in that pride gives the monthly per capita reproductive success for each size.

Figure 23.6b shows that there is considerable variation in per capita reproductive success of females in different-sized prides. Females in prides of three to ten had significantly more surviving cubs per month than those in either smaller or larger prides.

What is the cause of this relationship? Although most authors assume that the basic advantage of sociality to female lions is cooperative hunting, reanalysis of all the available data do not support this hypothesis (Packer 1986). Caraco and Wolf (1975) developed a model for estimating daily food intake by different-sized hunting groups from Schaller's (1972) data, and their analysis suggested that groups of two or three gain the highest rates of food intake per day. However, their model erroneously assumed that all

groups of two or more would have the same probability of capturing multiple prey in a single hunt and that hunting rate is independent of food intake. Schaller (1972) had found that groups of four or more made the highest proportion of multiple kills, and subsequently both Elliott, Cowan, and Holling (1977) and van Orsdol (1981) found that lions resume hunting more quickly after a small meal and thus that individuals with a lower success rate or smaller average meal size might compensate by hunting more often. When these assumptions were corrected, the model suggested that *solitary* females gain the highest food intake *per hunt* (Packer 1986). The model cannot be used to estimate *daily* food intake without data on group-size-specific hunting rates. An empirical assessment of daily food intake showed that females constrained to remain in groups of three or four adult females were thinner than those in groups of one or two, but that there were no differences across all pride sizes (Packer 1986). Females in large prides spend considerable time either alone or in small subgroups and are thus apparently able to forage as efficiently as members of smaller prides.

Further studies of hunting behavior are currently being conducted to test alternative hypotheses about the advantages of cooperative hunting. However, any advantages that may exist will have to be far greater than has so far been suggested to account for the higher per capita reproductive success of females in prides of three to ten. Both of the analyses above predict that rates of food intake will decline rapidly as hunting group size increases above one to three.

The results in figure 23.5 and table 23.4 show that infanticide is a major cause of cub mortality, and data on the frequency of male takeovers across all pride sizes suggest an important advantage to females from living in moderate-sized groups. Figure 23.6b includes the monthly probability of a male takeover in each pride size, and the relationship mirrors that of group-size-specific reproductive success. Not only do male takeovers result in the loss of a female's unweaned cubs, but females also take twice as long to conceive when mating with a new set of males (Packer and Pusey 1983a,b).

The higher takeover rate in smaller prides probably results from two factors: first, smaller groups of females are less able to defend their cubs against alien males (Packer and Pusey 1983a). Second, males generally annex small prides of females while they are still resident in a larger adjacent pride and continue to spend more time with the larger pride. The smaller prides are therefore more vulnerable to subsequent invasion. The takeover rate in larger prides may be higher because very large numbers of females attract many more males to their range. Larger groups of gelada baboons are similarly subject to higher takeover rates, and Dunbar (1984) showed that males preferentially select larger groups for their takeover attempts.

Female mortality is also higher for solitaries and pairs (fig. 23.6b), and this may be due in part to their higher rate of male takeovers. Several females have died in defense of their cubs (Packer and Pusey 1983a), and

females in small prides may be especially vulnerable during male attacks. Solitaries and pairs may also be subject to harassment from females in larger prides, but we lack direct evidence of this. Note that because of the high survival rates of females in each pride size, the relationship between female fitness and pride size is virtually identical to that between reproductive rate and pride size.

Although females apparently gain the same advantage from living in groups as males do, there is a striking contrast in their tendency to join unrelated companions. About half of all male coalitions include nonrelatives, but there is no case of unrelated females forming prides in these populations (Packer 1986). There appear to be greater constraints on females than on males in finding suitable partners. More than 33% of females leave their natal pride, and in comparison with females that remained there, dispersing females suffer lower reproduction rates in the Serengeti and higher mortality in Ngorongoro Crater (Pusey and Packer 1987). It is not known whether these costs of dispersal are directly due to the disadvantages of leaving a familiar area, but it is striking that dispersing females almost always settle in a portion of their natal range or an adjacent area (Pusey and Packer 1987). Familiarity with an area is likely to be especially important for successful reproduction in female lions through knowledge of suitable denning sites and good hunting areas; and such familiarity is most readily achieved by natal philopatry (Waser and Jones 1983). Thus solitary females may be unable to profit from a move to a new area to join another solitary or a pair. It is noteworthy that the only cases ever reported of unrelated females forming new prides followed a severe drought in the Kalahari Desert in which the natal areas of several females had become uninhabitable and they joined forces in a new area over 40 miles from their natal ranges (Owens and Owens 1984). Thus these females accepted unrelated companions when they were forced to range well away from their natal areas.

Why are lions the only social felid? The only advantage of group living that we have so far been able to detect is that moderate-size prides suffer lower rates of infanticide. Infanticide is an important source of cub mortality in lions, but it also appears to be common in tigers and mountain lions, and both of these species are solitary (Packer and Pusey 1984). Although female lions may not gain a strong positive advantage from cooperative hunting, the available empirical data suggest that the consequences of group hunting are at worst only mildly negative and are probably not as disadvantageous in lions as they would be in other species (Packer 1986). Thus in no other species might the advantages of group defense of cubs against infanticidal males be greater than the disadvantages of group foraging.

23.4 Summary

Long-term demographic data are presented on lions living in the Ngorongoro Crater and in Serengeti National Park, Tanzania. Variance in

lifetime reproductive success is higher in males than in females, and successful reproduction is confined to a narrower age range in males. Cub survival appears to be the most important variable affecting lifetime reproductive success of females. In males, cub survival and "fecundity" contribute equally to lifetime reproductive success. However, successful intercoalition competition is a necessary prerequisite for male reproduction. Considerable cub mortality is due to infanticide by incoming males and to starvation. Within each habitat, more cubs are reared in years with lower levels of male replacements, and hence less ·infanticide. Cub recruitment rates are higher where prey availability is greater. Cub recruitment is also higher when there are fewer adult females in each habitat. Adult females and subadult males in the area of highest population density, the Ngorongoro Crater, suffer higher mortality than their counterparts in either Serengeti habitat, but mortality of adult males is similar in all areas.

Males in large coalitions gain higher individual reproductive success. Solitary males readily join to form coalitions of two or three, but coalitions of four or more are always composed of relatives. Prides of three to ten adult females have higher per capita reproduction rates than smaller or larger prides, and these moderate-sized prides suffer fewer male takeovers. Females in prides of one or two females also suffer higher mortality. Unlike males, solitary females never form larger prides with unrelated companions. The evolution of female kin groups in lions is discussed.

23.5 Acknowledgments