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19. The Ecology of Sociality in Felids

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PERHAPS no mammals are as conspicuously solitary as members of the Felidae, yet the felids include one of the most remarkably social of all mammalian species: the African lion. Because almost all cat species are strictly carnivorous and females are solitary in all species except lions, comparison of the ecology of female lions with that of other felids should reveal the conditions that have resulted in lion sociality.[1] Until now, most reviews of felid sociality have ascribed group living in lions to the "advantages" of cooperative hunting of large prey (e.g., Schaller, 1972; Kruuk, 1972; Bertram, 1978, 1979; Gittleman, 1984; Macdonald, 1983). However, there has not been a convincing attempt to explain why cooperative hunting would be advantageous in lions but not in any other felid species. Furthermore, as shown below, the available data on hunting success in lions show that individual lions hunting in groups do not gain greater amounts of food than do solitary hunters.

In this chapter I briefly contrast lion social organization with that of other felids, compare preference for prey of large body weight across species, and test previous hypotheses about the advantages of group foraging in lions. I show that although females in moderate-size prides have higher reproductive rates (Packer et al., in press), group foraging does not confer obvious advantages in lions, and may even be disadvantageous under certain circumstances. I describe group dynamics in lions and suggest an alternative explanation for lion sociality. Since female lions do most of the hunting in the pride (Schaller, 1972) and it is the gregariousness of *female* lions that is so unusual among felids. I will be primarily concerned with the behavior and ecology of females. I briefly review gregariousness in male felids and contrast group formation in male lions with that of females.

FELID SOCIAL STRUCTURE

Since most solitary cat species show a similar social organization, I will first summarize the main features of the solitary species and then describe lion social organization in detail. Data on lions are based primarily on studies of

[1] I exclude domestic cats, which occasionally form social groups in households (Dards, 1978; Liberg, 1981), because the ancestral *Felis sylvestris* is always solitary, and because gregariousness may be a trait that has been favored by cat fanciers.

twenty prides in the Serengeti and Ngorongoro Crater, Tanzania. Two of these prides have been studied continuously since 1966 and the rest since 1974 (Schaller, 1972; Bertram, 1975a; Packer et al., in press). A. E. Pusey and I have studied these lions since 1978.

In all of the solitary cat species, females are intolerant of any conspecifics except their dependent offspring or males during the females' periods of sexual receptivity. In some species females have exclusive home ranges (tigers: Sunquist, 1981; bobcats: Bailey, 1974; lynx: Berrie, 1973; European wildcat: Corbett, 1979; servals: Geertsema, in prep.; and leopards: Bertram, 1982), while in others females have ranges too large to defend and thus their ranges overlap considerably (cougars: Seidensticker et al., 1973; jaguars: Schaller and Crawshaw, 1980; and cheetah: G. W. Frame, 1980). Although adult females may assist their maturing daughters to acquire a range near their own in some species (tigers: Sunquist, 1981; and possibly cheetah: Frame, 1980), no persistent associations between a mother and her mature daughter have been observed.

Female lions live in permanent "prides" consisting of two to eighteen related females, their dependent offspring, and a coalition of one to seven adult males that have entered the pride from elsewhere (Schaller, 1972; Bertram, 1975a; Packer and Pusey, 1982). Average pride size is similar across Africa (Van Orsdol, 1981). Male offspring are usually evicted with their fathers when a new male coalition takes over the pride, and sexually immature females are often evicted with them (Packer and Pusey, 1983a, 1984). Most females are recruited into their mothers' pride, but about 25 percent leave their natal pride at male takeovers or when their mothers give birth to a subsequent litter (Pusey and Packer, in press). Some females are solitary, being either the sole survivor of a pride (N = 2 cases in our study) or an individual evicted by incoming males before she had reached sexual maturity (four cases). If a solitary female successfully rears daughters, these may be recruited and the female returns to group living (Hanby and Bygott, 1979). However, there are no cases of unrelated females joining together to form a pride in our study areas (see also Table 19.3 below).

There is no apparent dominance hierarchy among females of a pride (Schaller, 1972; Bertram, 1979; Packer and Pusey, 1985). Unlike many other social carnivores, there is no reproductive suppression within the pride and all adult females typically breed at a similar rate (Packer and Pusey, 1983c, 1984). The number of surviving offspring per female is significantly higher in prides of three to ten adult females than in either smaller or larger prides (Packer et al., in press).

Pride females are often scattered in small groups throughout the pride's range and it is rare to find all pride members together. On average any two females of the same pride spend only 20-30 percent of their time together (Schaller, 1972). The fission-fusion nature of groups in a lion pride is illus-

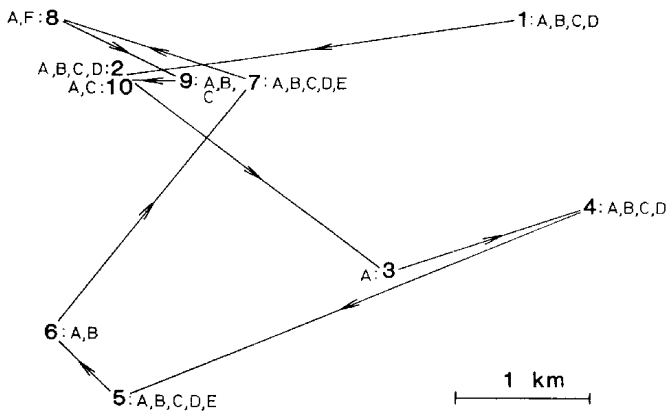

Fig. 19.1. Daily grouping and ranging patterns of Female A of the Gol Pride, Serengeti, 21–30 April 1980. Numbers refer to sightings on consecutive days and straight lines indicate changes in location. Letters B–F refer to the other five females in the pride. Females that were within 200 meters of Female A each day are listed next to that day's number.

trated in Figure 19.1, which shows the ranging and association patterns of an adult female over ten consecutive days. In this chapter the term "pride" refers to a set of individuals that regularly associates with each other (see Schaller, 1972), and "group" refers to a temporary aggregation of individuals from the same pride. Hence the female in Figure 19.1 was a member of a pride comprising six females and she was in groups ranging from one to five females over the ten-day period. Although their total range is too large to defend successfully, female lions do defend the portion of their range they currently occupy (Schaller, 1972). Pride ranges are stable over generations, and when prides split, the original range is subdivided (Pusey and Packer, in press). Solitary females also show stable ranges, but are often peripheral to their natal pride and thus range more widely.

Males are also solitary in most species, but typically have larger home ranges that overlap the ranges of several females (tigers: Sunquist, 1981; jaguars: Schaller and Crawshaw, 1980; cougars: Seidensticker et al., 1973; bobcats: Bailey, 1974; wildcats: Corbett, 1979). In contrast, male cheetah form stable coalitions of one to three males that defend territories much smaller than the ranges of females (Frame, 1980). Female cheetah are somewhat nomadic, ranging over very large areas, and male territories are found in areas utilized by a number of females (Frame, 1980). Coalitions of male lions defend female prides rather than a specific territory and large coalitions often "control" several adjacent prides simultaneously (Bygott et al., 1979; Pusey and Packer, 1983). Per capita reproductive success is higher in larger coalitions (Bygott et al., 1979; Packer et al., in press). Male-male relations are discussed in more detail in the final section below.

Schaller (1972) divided the Serengeti lion population into two categories: residents and nomads. Further observations in the Serengeti have shown that while most males have a nomadic phase, and may even remain nomadic for their entire lives if they never gain access to a pride (Bygott et al., 1979; Pusey and Packer, 1983), almost no females are truly nomadic. Subadult females may be evicted from their pride with subadult males, but the females either return to or settle near their natal pride (Pusey and Packer, in press). Adult females may leave their pride range temporarily either during extreme prey scarcity or while accompanying subadult offspring that have recently been evicted by new males (Packer and Pusey, 1983a, 1984), but they eventually return to their former range. Among Schaller's "nomadic females" were a number of females that moved over enormous areas of suboptimal habitat (the Serengeti Plains). Subsequent observations showed that when seasonal extremes in prey availability became less severe on the plains, these females were resident in the same areas (Hanby and Bygott, 1979). Therefore, when considering lion social organization, all females should be considered as showing a high degree of philopatry, although they may temporarily leave their usual range or expand their range under certain circumstances.

FELID ECOLOGY AND SOCIALITY: THE COOPERATIVE HUNTING HYPOTHESIS

Kleiman and Eisenberg (1973) pointed out that the stealthy hunting style of most felids virtually requires solitary living. Therefore the evolution of group living in lions requires an explanation. Bourliere (1963) noted that solitary carnivores typically prey upon animals smaller than themselves whereas social carnivores often capture relatively large prey. Kruuk (1972, 1975) developed this observation more fully and suggested that sociality itself may be an adaptation to capturing large prey. Predators would be better able to subdue large prey if they hunted cooperatively. Kruuk (1975) tested this hypothesis in each family of the Carnivora, but found that the predicted association between group living and a preference for large prey held well only in the canids and hyenids. Nevertheless, the lion's preference for large prey is the most commonly cited explanation for lion sociality.

Table 19.1 shows the ratio of *maximum* prey size to female body weight across all felids. Compared to other species, lions do occasionally capture prey very much larger than themselves (e.g., buffalo, eland, and giraffe). However, such very large prey comprise only a minor proportion of the lion's diet in many areas (Schaller, 1972, tables 36 and 37), and are typically captured by males rather than by females (Schaller, 1972, table 62; see also below). Therefore, a more relevant ratio would be based on the prey

TABLE 19.1
Relative prey size in felids

Species	Female weight (kg)	Prey size/ Female weight		References
		Maximum	Mode	
Lion *Panthera leo*	141.0	7.45	1.06	1, 2
Tiger *Panthera tigris*	143.8	2.78	0.52	3, 4
Jaguar *Panthera onca*	77.6	2.26	0.39	5
Cheetah *Acinonyx jubatis*	60.5	4.13	0.26	1, 6, 7
Cougar *Felis concolor*	46.4	6.17	2.44	8
Leopard *Panthera pardus*	32.7	3.98	1.08	1, 2, 4
Snow leopard *Panthera uncia*	31.7	2.46	1.26*	9
Lynx *Felix lynx*	12.7	2.25	0.12	10, 11, 12, 13
Caracal *Felis caracal*	9.7	3.40	<0.10	14
Serval *Felis serval*	8.8	5.23	<0.10	14, 15
Bobcat *Felis rufus*	6.2	7.25	0.30	16, 17
European wildcat *Felis sylvestris*	5.1	0.49	<0.10	18
African wildcat *Felis lybica*	3.9	0.64	<0.10	14, 19, 20

SOURCES: 1) Schaller, 1972; 2) Bertram, 1982; 3) Schaller, 1967; 4) Sunquist, 1981; 5) Schaller and Vasconcelos, 1978; 6) McVittie, 1979; 7) Frame and Wagner, 1981; 8) Hornocker, 1970; 9) Schaller, 1977; 10) Saunders, 1963; 11) Saunders, 1964; 12) Haglund, 1966; 13) Nellis and Keith, 1968; 14) Smithers, 1971; 15) Kingdon, 1977; 16) Gashweiler et al., 1960; 17) Gittleman, 1984; 18) Corbet and Southern, 1977; 19) Stuart, 1977; 20) Rowe-Rowe, 1978

NOTE: Ratio of maximum prey size to female weight excludes domestic prey species (e.g., water buffalo for tigers and reindeer for lynx) since these are unlikely to have been typical prey during the recent evolution of each cat species. Modal prey size is the size category most often taken by each species, and wherever possible is based on direct observations of prey capture, data from radio-collared animals, or from stomach/scat samples. Ad lib data are biased toward large prey (Bertram, 1979) and snow leopards are asterisked since all data were based on ad lib observations.

size preferred by females and Table 19.1 also shows the ratio of modal prey size to female body size. Cougars, leopards, and possibly snow leopards prefer prey that are even larger relative to their own body weight than do female lions. Thus, although lions are certainly at the high end of the spectrum, several other species would also be expected to be social if a preference for large prey was the *only* cause of sociality.

Even if lions did prefer the relatively largest prey, it would not be proof that lion sociality evolved as a consequence of the advantages of cooperative hunting: cooperative hunting may be an adaptation to group living, rather than the evolutionary force resulting in group living (see Alexander, 1974). Furthermore, the association would not necessarily implicate cooperative *hunting* (Kruuk, 1975). Groups may form in order to defend large carcasses either against conspecifics (e.g., coyotes: Bekoff and Wells,

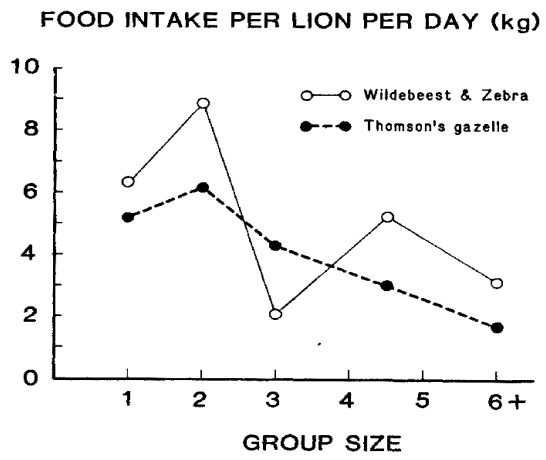

Fig. 19.2. Rates of daily food intake for individuals in different size groups while hunting either Thomson's gazelle or wildebeest/zebra, as calculated by Caraco and Wolf (1975). I have combined their results from wildebeest and zebra because Schaller's original data on hunting success did not differentiate between the two species. I have also included data on wildebeest and zebra for hunting groups of three; Caraco and Wolf intentionally excluded this point in their paper.

1980) or against other species (e.g., hyenas versus lions: Lamprecht, 1978b; but see below). Therefore it is essential to examine the available data on cooperative hunting in lions before accepting or rejecting the applicability of Kruuk's (1972) hypothesis to the felids.

COOPERATIVE HUNTING IN LIONS: THE CARACO-WOLF MODEL

Caraco and Wolf (1975) analyzed Schaller's (1972) data to estimate the optimal group size for hunting lions. Schaller had found that hunting success was twice as high for pairs as it was for solitary hunters, but that hunting success of three or more was no higher than that of pairs. Caraco and Wolf's analysis pointed out that it would be disadvantageous to be in too large a group because the captured prey would have to be divided into ever smaller portions while capture rate remained the same. However, groups do gain an added benefit since they can sometimes capture several prey simultaneously. Caraco and Wolf included a multiple-kill correction factor and determined the rate of food intake for each group size. According to their calculations, the hunting group size that maximized rate of food intake per individual per day would be two when hunting either Thomson's gazelle or medium-sized prey (wildebeest and zebra) (Fig. 19.2). In both circumstances their findings suggest that group hunting is optimal in lions since the optimal hunting group size is greater than one.

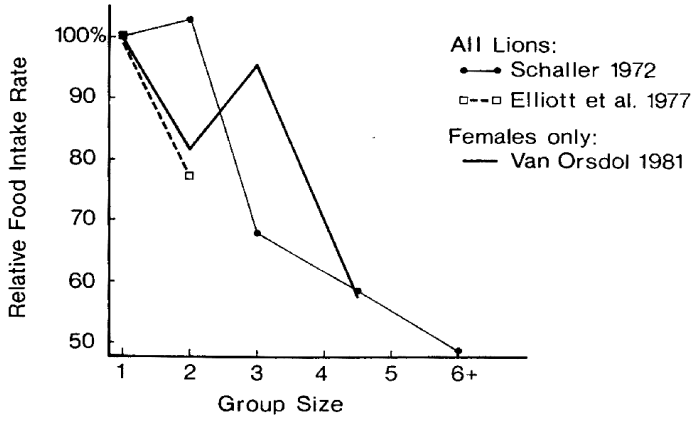

Fig. 19.3. Rates of individual food intake relative to that of solitary hunters, as calculated by the method described in the text. *Relative* rates of food intake are presented because it is the shape rather than the elevation of each curve that is of interest here and because it facilitates comparisons across studies. I have combined Schaller's 1972 (thin line) data on hunting success across all prey sizes. Hunting success does not vary significantly with prey size and thus the effect of hunting different-size prey affects only the elevation rather than the shape of the curve. Ideally, the data should be based on the number of females in each group (since they do most of the hunting), but only Van Orsdol, 1981 (heavy line) has presented such data. I have excluded Caraco and Wolf's "hyena loss" factor (which would award 10 percent greater levels of relative food intake to members of groups of > 4), since hyenas rarely steal *meat* from lions (see text).

Caraco and Wolf's model has been a very important and influential contribution, but unfortunately Schaller's data were not collected to test these hypotheses, and their model includes two assumptions that may invalidate the conclusion that group hunting is optimal in lions.

1). The multiple-kill correction factor. Caraco and Wolf awarded all groups of two or more the same proportion of multiple kills, although Schaller (1972, p. 254) stressed that the chances of making multiple kills were highest for groups of four or more. Consequently, the model overestimates the rate of food intake for groups of two and three, which is significant since the model shows the optimal group size to be two.

I have reanalyzed Schaller's data (as well as more recent data from other studies) using a multiple-kill factor that more closely approximates Schaller's findings. Schaller did not report the precise relationship between group size and proportion of multiple kills, but did give the average proportion of kills that included multiple carcasses (20.5 percent, excluding buffalo: 1972, table 42) and stated that most were made by groups of four or more. Thus I have assumed that the proportion of multiple kills increases linearly with increasing group size from 0 percent for solitaries to 33.3 percent for groups of six and more, which has the same mean across group sizes of two

or more as given by Schaller. Note that this still overestimates the proportion of multiple kills made by groups of two and three, but not as much as in Figure 19.2.

By this method, the estimated rate of food intake per individual per day is generally highest for lions hunting alone (Fig. 19.3). In some areas, pairs or trios may do as well as a solitary hunter, but overall it appears that lions would enjoy the highest rates of food intake if they were as asocial as any other felid!

2) Number of hunts per day is independent of food intake and of group size. Caraco and Wolf based their calculations on the assumption that a lion could hunt only three times per day, regardless of the levels of recent food intake or of the number of other lions in its group. J. P. Elliott et al. (1977) and Van Orsdol (1981) have since published data showing that hunting frequency increases with decreasing levels of food intake: hungry lions hunt more often. This finding essentially invalidates the results presented in Figures 19.2 and 19.3, since lions suffering from reduced food intake per *hunt* may be able to compensate merely by hunting more frequently each day (note that Figs. 19.2 and 19.3 actually indicate rates of food intake per *hunt* since it is assumed that all group sizes hunt with the same frquency). Unsuccessful hunts often involve exhausting chases and if only a few group members become exhausted during cooperative hunts, it would be especially likely that large hunting groups could compensate by hunting more frequently. However, data on hunting rates of different group sizes are not available.

Rather than end this section with the conclusion that solitary hunting maximizes rate of food intake in lions, I wish instead to emphasize that two types of data must be collected before Caraco and Wolf's model can be properly utilized. First, the average biomass of kills made by groups of different sizes (to replace the extrapolated multiple-kill factor), and second, the hunting rates of different-size groups. Note that both will have to confer very strong advantages to large groups if they are to account for the higher per capita reproductive success of females in prides of three to ten.

GROUP FORAGING AND FOOD INTAKE: ALTERNATIVE DATA

Although our own lion studies have not yet focused on hunting behavior, we do have extensive data on group dynamics and rates of food intake. We regularly censused twenty prides and made daily observations of feeding and grouping patterns from July 1978–May 1981, February–May 1982, November 1982–January 1983, and July–October 1983. Whenever we locate a lion or group of lions we note the identity of each individual, their "belly size" if they are standing (see below), and the age, sex, and species of any carcass upon which they are feeding. These observations are referred to as

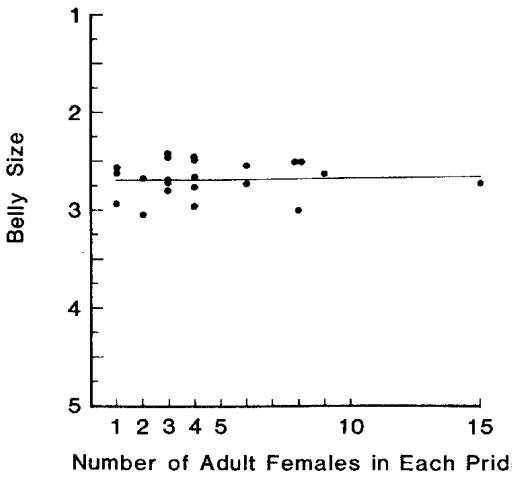

Fig. 19.4. Average belly size of females living in different sized prides. Each point is the mean across females of each pride. "Belly size" is based on a scale developed by Bertram (1975b) with 1.0 being the fattest possible and 5.0 the thinnest. When belly size is regressed against pride size, $r^2 = 0.0044$, $y = 2.6942 - 0.0036x$. Data are taken from sightings made on non-consecutive days and the belly sizes of each female were measured at least four times (range = 4–27). Data are from all study prides in the Serengeti and Ngorongoro Crater (1978-1981). Two prides contribute two points each since they were each observed at times when pride size differed markedly.

"sightings." We also collected detailed data on feeding behavior during watches of approximately two hours each at nearly one hundred kills.

The weight of stomach contents can be estimated visually from the profile of a standing lion's belly (Bertram, 1975b), and thus the levels of recent food intake of different individuals can be compared. Unfortunately "belly size" data have two important limitations. First, lions scavenge as well as hunt (Schaller, 1972; Kruuk, 1972), therefore without direct observations of how the lion acquired its food, belly size cannot be related to *hunting* success. Nevertheless, belly size does indicate *foraging* success and thus these data can be discussed in terms of group foraging. Second, belly size cannot be related to current group size. Figure 19.1 illustrates the ephemeral nature of group sizes within a pride, but belly size declines only gradually after a large meal. Therefore it is never certain whether a well-fed or poorly fed lion has joined a group before or after it has eaten.

However, certain aspects of lion social organization can be used to estimate the effects of group size on levels of food intake. First, our study includes prides ranging in size from two to eighteen adult females as well as a number of solitary females. Whereas females in large prides are able to form large groups, solitary females and those in very small prides can never do so. Therefore, if forming large foraging groups increases levels of food

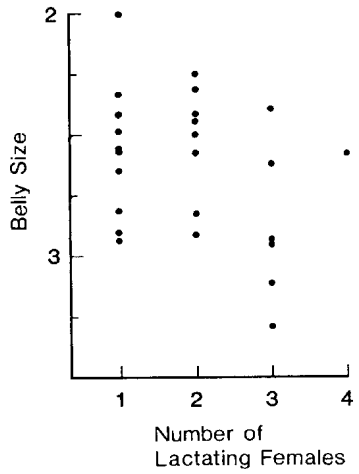

Fig. 19.5. Average belly size of lactating females rearing their cubs alone or communally. Each point is the mean across females of a set when all were lactating simultaneously (minimum of three measurements per female, range = 3–16). Age of cub does not have a significant effect on mother's average belly size. Singletons and pairs had significantly larger belly sizes than sets of three and four ($U = 26.5$, $n_1 = 18$, $n_2 = 7$, $p < 0.05$, two-tailed). Data are from all prides (1978-1983).

intake, belly size would be expected to increase with increasing pride size. However, there is no relationship between pride size and average belly size (Fig. 19.4), and thus solitary females and those in small prides do not suffer from reduced levels of food intake.

Second, females do not always alter group size as rapidly as the female in Figure 19.1. Females from the same pride with small cubs of similar age rear them cooperatively, and thus lactating females spend almost all of their time together (Schaller, 1972; Rudnai, 1974). Consequently, associations between lactating pridemates are much less variable than those between females in other reproductive states. As a result, average group size for mothers is set by the number of pridemates with similarly aged cubs rather than by characteristics of the food supply. In contrast to a nonlactating female in a large pride that might forage solitarily when prey size is typically small (Schaller, 1972, also see below), a lactating female in the same pride always remains in association with the other mothers. Thus lactating females are constrained to remain in groups with lower expected food intake, as predicted by Figure 19.2 and 19.3. Figure 19.5 shows that compared to singletons and pairs, sets of three and four mothers apparently suffer from lower levels of food intake.

The consequences of lowered food intake during lactation can be profound. The belly size of cubs is closely related to the belly size of their mothers ($r_s = 0.672$, $n = 15$ sets of mothers and cubs, $p < 0.01$) and poor

nutrition in cubs increases their mortality (cubs' average belly size versus percentage survival to twelve months: $r_s = 0.663$, $n = 13$ sets of cubs, $p < 0.05$).

In summary, females that are solitary or are members of small prides achieve rates of food intake similar to those of females in larger prides. Lactating females that are constrained by the presence of cubs to remain habitually in groups of three or four suffer from lower food intake than mothers that rear cubs alone or in pairs. Taken together, these findings suggest that group foraging decreases rates of food intake in female lions, but that the fission-fusion nature of the pride allows females to forage in smaller groups when necessary and thus females in large prides do not suffer reduced food intake.

Rather than a mechanism that improves food intake, communal cub rearing appears to be an adaptation against infanticide: groups of females are more successful than solitaries in defending their cubs against alien males (Packer and Pusey 1983a, c, 1984, in prep.). Small cubs are killed whenever new males enter the pride and moderate-size prides suffer lower frequencies of male takeovers than do smaller or larger prides (Packer et al., in press).[2] Although communal defense against infanticidal males may be an important advantage of group living in female lions, by itself it cannot explain the distribution of sociality across species: infanticide by males also occurs in tigers and cougars (see review in Packer and Pusey, 1984), but females in these species are nevertheless solitary. Communal rearing strategies will be examined in detail elsewhere.

OTHER POSSIBLE ADVANTAGES OF GROUP FORAGING

Maximizing the rate of food intake is not the only possible advantage of group foraging. Three other possibilities may confer an advantage to moderate-size prides over smaller prides.

1) Cooperative hunting minimizes risk of starvation by minimizing variance in food intake (see Caraco et al., 1980; Rubenstein, 1982). Schaller's data suggest that a single female has to hunt six times to ensure a single success, whereas groups need only hunt three times. When prey is so scarce that only one or two hunts can be attempted per day, a run of bad luck could be fatal to a solitary female. However, the data used in Figure 19.4 show *no* relationship between pride size and variance in belly size. Variance in belly size was calculated for each female and the average variance in each pride was regressed against the number of females in that pride ($n = 22$, $r^2 = 0.0002$). Nevertheless, if such a life-and-death situation occurred only once every year or two it would still be of great importance, though too rare to be

[2] The reason for the higher rate of male takeovers in very large prides is not clear, but may result from a far greater attraction of male coalitions to the range of such large numbers of females (see Packer et al., in press).

documented. The above data were collected over all times of year and seasonal variations in prey availability may have swamped any effect from group foraging. To test this hypothesis properly, extensive observations should be made of different size groups during periods of extreme prey scarcity.

2) Cooperative hunting decreases risk of injury during prey capture (Schaller, 1972; Kruuk, 1975). Schaller suggested that by hunting in groups, lions could prey on very large animals that would be too dangerous to a single hunter. In some areas (e.g., Manyara Park: Schaller, 1972; Kafue Park: Mitchell et al., 1965), large prey such as buffalo do comprise an important part of the lions' diet. However, there are no data on the success rate of different size groups in capturing buffalo, nor are there good data on risk of injury. Limited data on fatalities due to buffalo are available from our study. Between 1979 and 1983 one adult female in Ngorongoro Crater was observed being killed by buffalo (S. Trevor, pers. comm.) and three others were found dead and were assumed to have been killed by buffalo on the basis of their wounds and the trampling of nearby vegetation (pers. obs.; S J. Cairns and A. Geertsema, pers. comm.). These females were members of prides of two, three, four, and seven females respectively, suggesting that females in smaller than average prides have a somewhat higher risk of being killed by buffalo. However, the relationship is not statistically significant (proportion of Ngorongoro females killed in small prides [two out of ten] versus proportion killed in large prides [two of twenty-seven] $p > 0.20$, Fisher test), nor is it known if the females were killed while attempting to capture the buffalo. Buffalo will sometimes chase lions without provocation (pers. obs.).

As stated earlier, there are many areas where large, dangerous prey comprise only an insignificant part of the lions' diet, and thus I am skeptical of the importance of their safe capture in the evolution of lion sociality. However, even small to medium-size prey such as warthog, zebra, and wildebeest can occasionally injure a lion, and relatively minor wounds may reduce a female's subsequent hunting success (Bertram, 1978). Data are needed on wounding rates based on direct observation of prey capture, as well as data on the hunting success of wounded females. Also, group hunts may typically require shorter chases and thus not only be less energetically expensive but also result in less wear and tear to each hunter.

3) Group foraging increases success in competition with spotted hyenas (Schaller, 1972; Lamprecht, 1978b; Eaton, 1979). Lions and spotted hyenas have very similar prey preferences, and often compete over carcasses (Kruuk, 1972; Schaller, 1972). Lions are dominant to hyenas, except in encounters between few (1–2) lions and many (20-40) hyenas. Schaller found that 44 percent of carcasses fed on by lions are eventually lost to hyenas. But are these losses substantial enough to account for group living

in lions? Schaller (p. 272) found no striking relationship between the number of lions feeding at a carcass and the probability of losing it to hyenas (and Fig. 19.4 suggests that solitary female lions forage as successfully as group-living females). Furthermore, almost all published observations, as well as our own, show that lions surrender only the remnants of a kill (i.e., skin and bones) after they have gorged themselves on the meat. The crucial question is whether a female lion feeding solitarily loses more meat to hyenas than a lion feeding socially loses to her companions. Data presented in the next section show that lions lose considerable quantities of meat to conspecifics. In contrast, the quantity of *meat* lost to hyenas was negligible. During our detailed observations of lions feeding at ninety-one carcasses, the lions lost only two carcasses to hyenas when more than 10 percent of the meat was remaining, and Van Orsdol (1981) reported a similar finding. Although primarily meateaters, hyenas are also adapted to eating large bones (Kruuk, 1972), whereas lions will only eat the bones of small or immature prey. However, lions will sometimes spend hours gnawing at bones, removing the last traces of meat, and it is then that hyenas become boldest and try to take them away from the lions. This is presumably because the remains have become more valuable to the hyenas than to the lions.

In summary, the minimization of risks of starvation and injury may eventually prove to be important advantages of cooperative hunting in lions, but supporting data are not yet available. Competition with spotted hyenas does not appear to be an important advantage of group foraging in lions. However, even if both minimizing the risks of starvation and injury prove advantageous, detailed data from other felids would be required to show why these factors have resulted in sociality only in the lion.

LION GROUPING PATTERNS AND PREY SIZE: AN ALTERNATIVE VIEW

Prey size appears to be one of the most important variables determining group sizes within a lion pride (Schaller, 1972; Caraco and Wolf, 1975). However, this is primarily because a large carcass attracts a large number of lions. It is difficult to estimate *hunting* group size without direct observations during the moment of prey capture. Most published data are on *feeding* group size. We likewise lack good data on hunting group size and in the following analysis, I attempt to provide reasonable estimates of hunting group size as well as direct measures of feeding group size in order to measure the precise effect of prey size on group size.

Where prey size varies seasonally, consecutive kills will tend to be of the same prey species and hence of similarly sized prey. Therefore, group size prior to prey capture can be assumed to reflect preferred hunting group size for prey of a particular body size since the group will be likely to encounter

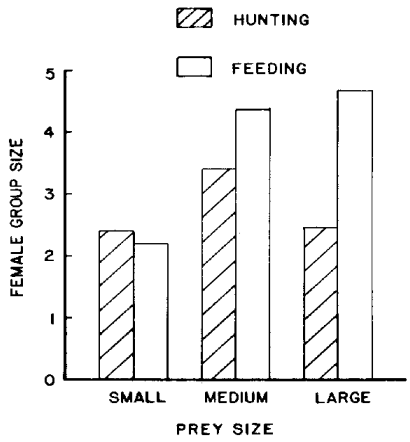

Fig. 19.6. Effect of different-size prey on female group size in the Masai Pride. Small prey include all species with adult weight < 100 kg (e.g., gazelle and warthog); medium-size prey, 100–250 kg (e.g., wildebeest and zebra); large prey, > 300 kg (e.g., buffalo, eland, and giraffe). Hatched bars refer to group sizes within two days before or after a kill of a particular size, but not in the presence of a carcass. These are assumed to reflect hunting group sizes. Open bars are group sizes in the presence of a carcass and thus show feeding group sizes. There was significant heterogeneity ($p < 0.01$, Kruskal-Wallis) both in hunting ($n = 276$ sightings) and feeding ($n = 86$) group sizes of different-size prey species. Feeding group sizes are significantly larger than hunting group sizes ($p < 0.01$) for both medium-size and large prey. There is no significant difference between hunting and feeding group sizes for small prey ($p > 0.20$). Data are from 1978–1981, during which time the Masai Pride included an average of fifteen females.

consecutive prey of the same species. Seasonality of prey size is particularly striking in the Masai pride, one of Schaller's original study prides and the one on which much of the Caraco-Wolf analysis was based. This pride mostly captures medium-size prey from November to May, when the migratory herds are present in their range, and females mostly take small prey during the remaining months (the males occasionally catch buffalo during this same period). Figure 19.6 shows the average group size of the females in the Masai pride during periods when prey of different sizes were available, and the influence of the presence of carcasses of different sized prey on group size. Although females in this particular pride were in the largest hunting groups when medium-size prey were the primary food source, the increase following the capture of a large or medium-size prey was even more pronounced.

The increase in group size in the presence of a medium or large carcass occurs because many lions eventually arrive to feed at the carcass: the presence of a kill is the most common context in which female pridemates meet (Fig. 19.7). The larger the carcass, the longer it persists (edible biomass of

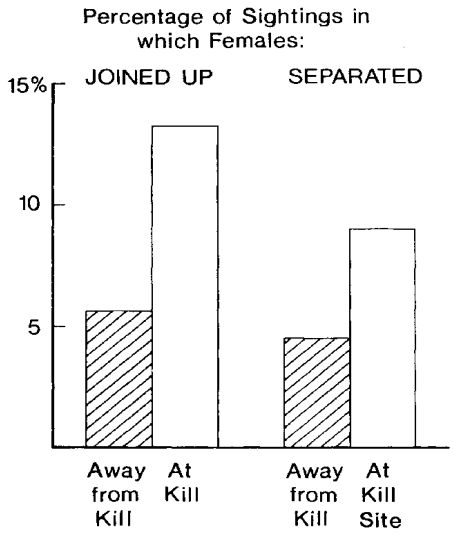

Fig. 19.7. Effects of the presence of a carcass on females moving into proximity of each other. A female is significantly more likely to move to within 200 meters of another female when the latter is at a kill (one sample $\chi^2 = 12.67$, 1 *df*, $p < 0.001$, $n = 70$ sightings in which females joined). Females also separate more frequently after feeding ($\chi^2 = 5.38$, $p < 0.05$, $n = 53$), emphasizing that feeding groups are often just temporary aggregations. Data are from all prides (1978-1981).

all kills at a site versus time from onset of feeding until 90 percent is consumed: $r_s = 0.792$, $n = 38$, $p < 0.001$, range = < 5 minutes for a 2-kg carcass to > 2 days for a 500-kg carcass). Consequently, more lions will be likely to locate and feed from a larger carcass. However, on the rare occasions when a carcass remains undiscovered by the remainder of the pride, one or two individuals may feed from a medium-size carcass for several days.

A female can often monopolize a small carcass (in competition with other females), but is much less successful in preventing other females from joining her on a medium or large carcass (Fig. 19.8). Therefore, a medium or large carcass is readily accessible to latecomers. It is important to recall that there is no dominance hierarchy among females at a kill. Instead, latecomers respect the first female's "ownership" of a small carcass or of a specific site at a larger carcass (Packer and Pusey, 1985). A larger carcass has many more acceptable feeding sites and the first female defends only her own site rather than the entire carcass.

Not only does a carcass attract pridemates, it also attracts individuals from other prides. Most interpride encounters occur at kills (Fig. 19.9). Females are intolerant of strange females within their range and interpride en-

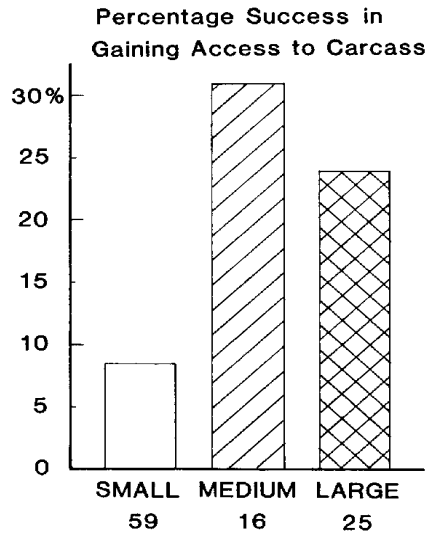

Fig. 19.8. Proportion of attempts by females to join a feeding female on a kill that were successful in spite of being threatened by the feeding female. Effect of size class of prey species is significant ($G = 6.26$, 2 df, $p < 0.05$). Numbers below size classes are the number of times a feeding female threatened a second female that attempted to join her at the kill. Data are from detailed observations of feeding lions in all prides (1978–1983).

counters usually end either with the larger group of females chasing away the smaller or the smaller group spontaneously avoiding the larger. However, if an interpride encounter occurs at a kill, the females finish feeding before chasing each other. Thus although females will defend their range against intruders, they do not cooperatively defend individual carcasses. On four occasions females from different prides were seen actually feeding together (on the carcasses of an elephant, giraffe, buffalo, and warthog). Similar large, temporary aggregations at very large carcasses have been observed in cougars (Seidensticker et al., 1973) and provisioned tigers (Schaller, 1967).

These data emphasize the importance of large prey size on gregariousness in lions: individuals aggregate at large kills. But as a result considerable meat is lost to conspecifics that were not present at the time of the kill—meat that could have been eaten by those who captured the prey if the latecomers could have been excluded.

The data in Figure 19.6 show that hunting group size is largest when females are hunting medium-size prey, the heaviest prey regularly captured by females of this particular pride (most of the large prey were believed to have been captured by the adult males). This finding can be interpreted in at least two ways. First, medium-size prey require cooperative hunting by the females, perhaps because of reduced risk of injury. Second, once they have

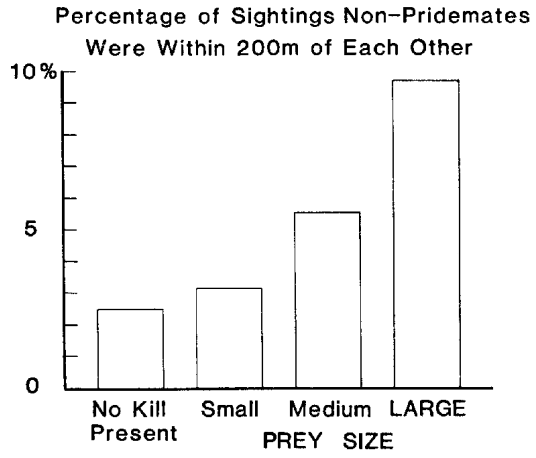

Fig. 19.9. Effect of the presence of carcasses of different sizes on the frequency of interpride encounters (one sample $\chi^2 = 14.91$, 3 *df*, $p < 0.01$, $n = 94$ interpride encounters). Data include observations involving all age-sex classes and all prides (1978–1981).

been captured, medium-size prey provide sufficient meat for more females than do small prey and thus being a member of a larger group is less costly than when hunting small prey (Caraco and Wolf, 1975; Kruuk, 1975). Large aggregations that had formed at larger carcasses would therefore be more likely to persist until the next prey is captured.

THE EVOLUTION OF GROUP LIVING IN LIONS

A large carcass is perhaps the ultimate large, ephemeral, and patchy resource. Enough meat is available to feed several lions, but is consumed within a day or two, and at any given time there may be only a few carcasses available over a wide area. The lion's diet therefore shows a fundamental similarity to that of many other social vertebrates (e.g., weaverbirds: Crook, 1964; primates: Clutton-Brock and Harvey, 1977; carnivores that specialize on small, patchily distributed prey: Kruuk, 1978b; Macdonald, 1983). Why among all the felids are only lions social?

I suggest that lion sociality results from the unique combination of three factors: preference for large prey, openness of habitat, and high population density. Table 19.2 shows that lions are the only felid to show extremes for all three of these variables. The consequences of a preference for relatively large prey are emphasized in Figures 19.6 and 19.8: large prey size allows several individuals to feed from the same carcass. How do an open habitat and high density relate to lion sociality? Open–country species live in larger groups than forest species in many mammals (antelopes: Jarman, 1974; primates: Clutton-Brock and Harvey, 1977; carnivores: Gittleman, 1983) and

TABLE 19.2
Relative prey size, density, and typical habitat of felids

Species	Modal prey size/Female wt	Female density (per 100 km^2)	Habitat	References
Lion	1.06	7.9	Open savannah	1, 2
Tiger	0.52	2.7	Forest	3, 4, 5
Jaguar	0.39	3.1	Forest	6
Cheetah	0.26	2.9	Open grassland	1, 7, 8
Cougar	2.44	0.7	Woodland/brush	9, 10, 11
Leopard	1.08	2.9	Forest/brush	1, 12, 13
Snow leopard	1.26	1.0	Forest/brush	14
Lynx	0.12	5.9	Forest	15, 16
Bobcat	0.30	7.1	Forest/brush	17–22

SOURCES: 1) Schaller, 1972; 2) Van Orsdol et al., in prep.: 3) Schaller, 1967; 4) Borner, 1978; 5) Sunquist, 1981; 6) Schaller and Crawshaw, 1980; 7) Eaton, 1974; 8) Frame and Wagner, 1981; 9) Hornocker, 1969; 10) Hemker, 1982; 11) Hopkins et al., 1982; 12) Muckenhirn and Eisenberg, 1973; 13) Bertram, 1982; 14) Schaller, 1977; 15) Saunders, 1963; 16) Berrie, 1973; 17) Provost et al., 1973; 18) Bailey, 1974; 19) Fendley and Buie, 1982; 20) Lancia et al., 1982; 21) Lembeck, 1982; 22) Litvaitis et al., 1982

NOTE: Modal prey size is from Table 19.1. Female density is the median value across study sites and is based on the number of adult females over a given area, except in lynx and bobcat. Direct estimates of female density were unavailable for these species and are instead based on the inverse of home range size, since females have nonoverlapping home ranges. Thus, densities for these two species are probably too high. Estimates of density of cougars and snow leopards are probably too low since both suffer from intensive hunting pressure by humans except in marginal habitat.

this relationship is usually attributed to improved protection against predators—an unlikely explanation in the case of the lion. It has also been suggested that open habitat allows the coordination of group hunting by lions (Sunquist 1981, Gittleman, 1983). However, Van Orsdol (1981) found no relationship between degree of cover and hunting group size, which suggests that lions do not engage in cooperative hunting more often in open areas.

Openness of habitat has another consequence: a carcass is much more conspicuous to vultures and to mammalian scavengers, including lions. Lions watch for vultures, particularly when prey is scarce, and they will travel several kilometers to where vultures have landed. A lion at a kill can also be seen from far away, and lions will join feeding pridemates from several kilometers away. In contrast, Sunquist (1981) found it difficult to locate tiger kills visually, even from short distances, because of dense vegetation. Schaller (1972), Van Orsdol (1981), and ourselves have all noted that lions sometimes move carcasses from open areas in an apparent attempt to conceal them. Large carcass size ensures that food will still be available by the time scavenging lions arrive: a small carcass would have been consumed. Thus in species such as the cheetah, which also live in open country but spe-

cialize on relatively small prey, intraspecific scavenging would be less rewarding than in lions. In fact, cheetah almost never scavenge from each other (T. Caro, pers. comm.).

Throughout almost all of their range, lions live at higher densities than any of the other big cats. The lion's preferred prey species are all typically found in large concentrations and I suggest that high lion density is a prerequisite to sociality rather than its consequence. As a result of high density, lions are particularly likely to suffer losses of meat to conspecifics: a kill made by a single lion would be likely to attract many other lions simply because there are more lions in the vicinity. Therefore, there is greater scope for females to come into close proximity in lions than in any other large felid.

Furthermore, at high population density a dispersing subadult female might have more difficulty in establishing a new range (see Emlen 1982a, b). It will be impossible to determine whether costs of dispersal in lions are higher than in other species, since it is the costs of leaving relative to those of staying that are important and in no other felid species do females remain with their mothers. However, dispersing female lions do have lower fitness than females that are incorporated into their natal pride and the costs of dispersal are more severe in areas of higher population density (Pusey and Packer, in press). Dispersing females in Ngorongoro Crater suffer higher mortality than nondispersers; whereas dispersing females in the Serengeti have lower reproductive rates than nondispersers, but do not suffer higher mortality. Population density in the Crater is two to four times higher than that in the Serengeti.

The lion's preferences for large prey size and open habitat, and their high population density, may have resulted in sociality in the following manner. An ancestral female lion that was as solitary as any other felid was confronted with the ecological conditions of a modern lion. She typically captured prey that were similar in size to her own body weight and the carcasses regularly attracted other females to the site of the kill (Figs. 19.7-19.9). As her daughters approached maturity, their continued association with her slightly depressed her rate of food intake (Fig. 19.5). However, the costs of dispersal may have been so high relative to these losses that the mother would have increased her inclusive fitness by allowing the daughters to remain in her range (see Rodman, 1981). Furthermore, if the mother and her mature daughters subsequently associated as sporadically as do modern pridemates (Fig. 19.1), but their ranges overlapped so that the mother's contact with nonrelatives became less frequent (Waser and Jones, 1983), then the initial disadvantage of group foraging might have disappeared (Fig. 19.4). In addition, any loss of meat to her daughters would have been compensated by the fact that it was lost to close kin rather than to more distantly related neighbors (W. D. Hamilton, 1964). The mother could not dominate

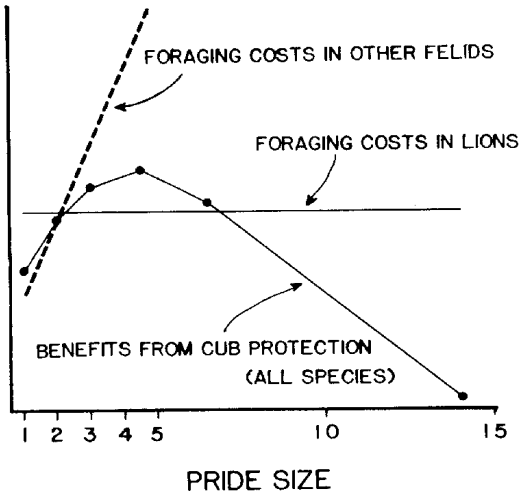

Fig. 19.10. Costs and benefits of sociality in lions and other felids. The benefits of cub defense are the inverse of the frequency of male takeovers for each pride size (from Packer et al., in press). The pride size with the lowest frequency of male takeovers suffers the lowest incidence of infanticide, and hence gains the greatest benefits from sociality. I assume that this pattern would be similar in other felids if they were also social. The "costs" of foraging are the losses of meat to conspecifics by females in different sized prides. In lions these costs are based on Figure 19.4 but are conjectural for other species. The elevations of these curves are drawn so that optimal pride sizes are given by the regions where the benefits of cub defense exceed the costs of foraging: 3–7 in lions (against an observed of 3–10) and 1 in other felids. Solitary females of other felids are also assumed to suffer lower foraging "costs" than do solitary female lions (see text).

her mature daughters (Packer and Pusey, 1985) and thus could not prevent them from breeding even if it was in her best interests to do so (see Vehrencamp, 1983). Once the mother and daughters reared their cubs communally in order to defend them against infanticidal males, then a modern pride had been achieved.

In contrast, female leopards or cougars (which often take large prey but live at much lower densities) gain greater benefits from living alone: they are unlikely to lose meat to unrelated conspecifics and would thus suffer a much greater reduction of food intake by allowing their daughters to remain within their ranges. Thus the costs of group foraging both to the mother and to the daughters may outweigh any advantage of cooperative cub defense.

In Figure 19.10 I have plotted the observed relationships of food intake rate and risk of infanticide across all pride sizes in lions, and have also plotted the hypothetical relationships for an ordinarily solitary felid. I assume that the advantages from cooperative defense against infanticidal males in most solitary species would be the same as in lions, but that food intake would decrease rapidly with increasing "pride" size in the solitary species.

I have also assumed that solitary females of the solitary species have a higher feeding efficiency than solitary female lions because they do not lose as much meat to conspecifics. Lions may be the only species in which females are able to gain a net advantage from sociality because they are neither able to benefit from solitary foraging, nor suffer prohibitive costs from group foraging.

There are three important predictions from this analysis for which we do not yet have adequate data. First, solitary females should lose comparable quantities of meat to other lions as do pride-living females. Second, losses to conspecifics by solitary female lions should also be higher than those suffered by females in other species. Third, female lions should show a greater tendency to be solitary in areas of low population density. All available data on the number of females per pride are from areas where the population density is nearly an order of magnitude higher than that of other large felids. However, the only areas where lions occur at very low density are extremely arid (e.g., parts of the Kalahari desert: Eloff, 1973), and thus lions may aggregate anyway at waterholes (see Macdonald, 1983).

Conversely, females of other species should show greater gregariousness in areas of high density. Although there are no good data on this point in other felid species, supporting data are found in other carnivore families. Spotted hyenas are found at higher densities and prefer larger prey than either striped or brown hyenas and are the most gregarious of the three species (Kruuk, 1972, 1976; Owens and Owens, 1978). Kruuk's (1972) study of spotted hyenas illustrated how huge aggregations could form at large kills and that cooperative hunting played a relatively minor role in prey capture. Female white-tailed mongooses forage solitarily for insect prey but their ranges overlap extensively with their mother's range in areas of high density, whereas females have nonoverlapping ranges in areas of low density (Waser and Waser, 1985).

Group territoriality may also be favored in situations where the presence of a few additional animals does not seriously deplete resources and where there is a moderately high level of intruder pressure (Davies and Houston, 1981; J. L. Brown, 1982). Although much of the data presented in this chapter are consistent with this idea and female lions do show cooperative range defense, I have not emphasized group territoriality for two reasons. First, since it does not directly involve defense of carcasses, we cannot easily quantify the precise consequences of such behavior. Second, there is no apparent relationship between rate of food intake and pride size (Fig. 19.4) as would be expected if group territoriality increased feeding efficiency. However, group defense may result in reduced hunting frequency and thus reduce injury rates and energy expenditure during prey capture. Studies are in progress both on cooperative territorial defense and on cooperative hunting.

TABLE 19.3
Kinship in male coalitions and female prides

	Always composed of close relatives	Ever include nonrelatives
Male coalitions	8	9
Female prides	19	0

NOTE: Based on male coalitions of known origins that gained access to female prides between 1978 and 1983, and on the composition of female prides in 1983 which had recruited members after 1975. $p < 0.001$, Fisher test.

SEX DIFFERENCES IN KINSHIP PATTERNS IN LIONS

In both sexes, individuals gain mutualistic reproductive advantages from group living: per capita reproductive success of male coalitions increases with increasing coalition size and is at a maximum in prides of three to ten adult females (Packer et al., in press). However, there is a striking difference between the sexes in their choice of companion in our study areas: whereas males frequently form coalitions with unrelated partners, females of the same pride are always close kin (Table 19.3). It is not surprising that solitary males and pairs of males join up with unrelated partners, since each male can thereby increase his reproductive success (Packer and Pusey, 1982, 1983b).[3] However, it is puzzling that solitary females do not form larger prides with other solitaries or pairs.

This sex difference may result from the differing consequences of philopatry and dispersal to each sex. Large male coalitions gain higher reproductive success because they are more likely to gain access to a pride, gain larger prides, and control prides for longer periods (Bygott et al., 1979). None of these factors depends critically on familiarity with an area: males maintain exclusive access to a set of females rather than to a range. Thus a solitary or pair of males can move over great areas in search of companions and settle in any pride they can take over (Pusey and Packer, in press). In contrast, females almost never move substantial distances from their natal range. Even those that are not incorporated into their mothers' pride nevertheless remain in a portion of their natal range or in an area immediately adjacent to that range. It is not known whether the lower reproductive success of these dispersing females results from a loss of access to all or part of their natal range, but it seems likely that they must learn the location of new safe denning sites and good hunting areas during critical times of year (see

[3] Coalitions of male cheetah are also often composed of nonrelatives (Frame, 1980), but the consequences of cooperation for each male are not yet known.

also Waser and Jones, 1983). Therefore, there may be real constraints that prevent females from leaving their natal area to find additional companions.

The only known cases of unrelated females forming new prides lend some support for this idea. After a severe drought, a number of females in the Kalahari Desert moved over forty kilometers to a new area and several solitaries formed new prides with nonrelatives (Owens and Owens, 1984). Once the females had been forced to disperse to a new area they were then willing to accept unrelated companions. In our study areas, we have twice seen pairs of unrelated solitary females in close and apparently amicable association outside their usual ranges. However, in both cases the two females returned to their respective ranges shortly thereafter and continued to live as solitaries.

CONCLUSIONS

The evolutionary causes of lion sociality are complex, but the distribution of sociality in felids shows many similarities to other taxa of higher vertebrates. Obviously, more data are needed to ascertain the effects of cooperative hunting on food intake, injury rate, and risk of starvation; but the available data suggest that group living has evolved in spite of disadvantages of group hunting. Although solitary foraging may yield the highest rate of food intake to *hunting* lions, scavenging is particularly profitable in this species and thus large groups often form at kills. Consequently, the average rate of food intake is independent of pride size, and across all felids only female lions can form stable subgroups to defend their cubs against infanticidal males. The kin-biased structure of female prides apparently results from high levels of natal philopatry.