Why Lions Form Groups: Food is Not Enough

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Most studies of animal grouping patterns assume that living in groups confers a wide variety of costs and benefits (see, e.g., Bertram 1978a; Caraco 1979; Caraco et al. 1980; Pulliam and Caraco 1984; Elgar 1987). However, a number of recent papers on the grouping patterns of wild African lions have focused exclusively on a single factor: group-size-specific foraging success. Empirical studies of grouping that focus on a single factor have been most successful when conducted in controlled laboratory settings (e.g., foraging-group size in sticklebacks; Milinski 1979). Where changes in group size have conflicting effects, an individual's decision to join or leave a group of a particular size must weigh different factors (see Pulliam and Caraco 1984). For example, if feeding efficiency is maximized by solitary foraging but each individual's risk of predation is reduced by the dilution effect, the group size that maximizes individual fitness may be larger than one (Terborgh and Janson 1986).

Lions would seem to be ideal subjects for grouping studies because they live in fission-fusion social units (prides) that allow pride members to form subgroups of differing sizes. However, lions not only engage in group foraging but also defend their young and their territories as a group (see Schaller 1972; Bertram 1978b; Packer 1986). In species that engage in a variety of group-level activities, decisions concerning grouping patterns are likely to be highly complex. It is therefore not surprising that attempts to predict the grouping patterns of the Serengeti lions have led to considerable controversy.

The first attempt to relate lion grouping patterns to foraging success was made by Caraco and Wolf (1975). Using data collected by Schaller (1972), they estimated that individuals hunting in groups of two gain the highest rate of food intake. However, Schaller's data on group size showed that lions typically forage in groups larger than would be predicted on the basis of the rate of energy maximization. Caraco and Wolf concluded that other benefits of sociality might be sufficient to overcome the disadvantages of hunting in excessively large groups.

Subsequently, a number of authors sought to explain the apparently excessive group sizes of lions exclusively in terms of foraging. First, it was suggested that

because pride mates are close kin, lions should often forage in groups somewhat larger than predicted by a simple optimality analysis (Rodman 1981; Giraldeau 1988; Giraldeau and Gillis 1988). If moderate-sized groups gain the greatest food-intake rates, groups should sometimes accept additional members in order to prevent close relatives from incurring the costs of foraging alone. Second, because variance of food intake may often decline with increasing group size, group size is an important variable for risk-sensitive foragers (Pulliam and Caraco 1984; Clark 1987; Houston et al. 1988). As long as the average individual food-intake rate exceeds the animal's daily requirement, the risk of starvation would be minimized by choosing the group size with the lowest variance relative to its mean. Finally, it has been pointed out that an optimal group size may not be stable when pride mates are freely able to join and leave a foraging group. If groups gain higher rewards than solitaries, solitaries are expected to join larger groups until the group's size is so excessive that per capita payoff in the group no longer exceeds that of a solitary (Sibly 1983; Pulliam and Caraco 1984; Giraldeau 1988; Giraldeau and Gillis 1988).

Although there have been numerous attempts to reconcile the discrepancy between the observed group sizes and those predicted by Caraco and Wolf, any analysis based on Schaller's data is inadequate to test predictions of group foraging (Packer 1986). First, the only data that Schaller provided about the relationship between group size and feeding success concerned group-size-specific hunting success. Lions frequently acquire food by scavenging. Second, Schaller did not provide data concerning hunting frequency. All analyses have assumed that hunting rates are independent of hunting success and of group size, but Elliott et al. (1977) and Van Orsdol (1981) showed that hungry lions hunt more often. Third, as outlined below, Schaller's data on grouping patterns are inappropriate to test these hypotheses.

We present new data collected specifically to examine the relationship between foraging success and grouping patterns of female lions. We show that group-size-specific foraging success is insufficient to account for the observed distribution of group sizes. The grouping patterns of female lions result from a variety of factors, in particular, the demands of protecting their young and maintaining a long-term territory.

METHODS

Lions have been studied continuously in the Serengeti National Park, Tanzania, since 1966, and details of the population and habitat are available elsewhere (Packer et al. 1988). Beginning in 1984, at least one female in each of 21 prides was radio-collared. Radio-tracking with night-vision goggles permitted observation of females for up to 96 consecutive hours just before or following each full moon, for a total of 3,500 h between September 1984 and December 1987. These prides consisted variously of 1–11 females, 0–13 cubs, and 0–9 adult males. Analyses are based on the number of females older than 2 yr of age. Females do almost all of the hunting and are competent hunters by this age. All radio-collared females were as closely matched in age as possible and were observed only when they were not in estrus.

Pride mates can be scattered over an area of 100 km^2, but those in the same vicinity generally remain within a few meters of each other. We define a female "group" as all females from the same pride that are less than 200 m apart. We consider all groups foraging groups. Hunting by lions is extremely opportunistic: they not only search actively for prey but capture unwary prey that wander too close to them (Schaller 1972). Opportunities for scavenging can also arise at any time. During our study, meals were acquired at all times of day, and the intervals between meals followed a negative-exponential distribution. Not all females in each group participated in each hunt, but all fed from each carcass, and thus all lions in each group are foragers. If foraging success influences each individual's decision to join or leave a group, then that decision should depend on its group-size-specific foraging success. Once an individual is a member of a group of a particular size, whether or not to participate in a cooperative hunt is a separate decision (see Packer and Ruttan 1988). Data on group hunting will be presented elsewhere (Scheel, unpublished manuscript).

The quantity of meat from all meals (both scavenged and captured) could be accurately estimated from published data on carcass weight and composition for each age-sex class of prey (Sachs 1967; Ledger 1968; Blumenschine and Caro 1986). In the following analyses, *food intake* refers to the amount of meat actually consumed by the lions. This was calculated by estimating the edible biomass of the carcass when it was first acquired and subtracting from that quantity the carcass biomass at the completion of the meal. Each carcass was assumed to be divided equally among females because (1) social dominance does not occur among female pride mates (Schaller 1972; Bertram 1978b; Packer and Pusey 1985), (2) female pride mates have equal access to carcasses (Packer and Pusey 1985), and (3) females of the same pride show no significant inter-individual variation in recent food intake as judged by belly size (Pusey and Packer, unpublished data).

If adult males, lions from other prides, or hyenas appropriated the carcass from the female(s), meal size was adjusted accordingly. On the rare occasions that males fed with females, each male was assumed to eat twice as much as each female. Van Orsdol (1981) found that a male consumes twice as much meat, on the average, as a female when males and females feed from the same carcass. In the data presented here, meal size was not adjusted according to the number of cubs present. Less than a third of the foraging groups contained cubs and only 22% of females were mothers. Cubs were present in a similar proportion of groups of each size. Immatures fed from only 21% of carcasses, and it is difficult to estimate the precise food intake of cubs of different ages. However, in a second analysis, we estimated the food intake of immatures as follows: each cub less than 1 yr of age was assumed to consume one-third as much as each adult female; and each subadult 1–2 yr of age was assumed to consume two-thirds as much. This probably overestimates the consumption by immatures (Van Orsdol 1981) and thus gives a conservative estimate of food intake by females. The two analyses give virtually identical results for the effect of group size on food intake by females. We present only the results from the first analysis, because it indicates the amount of meat that each female successfully procured for herself and her dependent young.

Rates of food intake were calculated on a day-to-day basis; and variance is based on these daily measures. For statistical tests, data collected during each continuous observation period were averaged and treated as a single independent point. All tests are nonparametric because the data could not be normalized. All P values are two-tailed.

Data on foraging and grouping are presented separately according to two conditions.

1. The season of *prey abundance* occurs when large herds of migratory wildebeest, zebra, and gazelle are present within the ranges of the study population (see Sinclair and Norton-Griffiths 1978; Durant et al. 1988). Lions feed almost exclusively on the migratory species when they are plentiful. Food is so abundant under these conditions that females would often only partially consume a carcass before voluntarily abandoning it. In this study, prey abundance for most prides occurred from November to January and from May to June each year; for some prides, prey abundance persisted from November to June.

2. *Prey scarcity* occurs when the migratory herds are absent. Cub starvation is most common at these times (Packer et al. 1988), and hence, food intake is most relevant to female fitness. During prey scarcity, lions feed on almost any species (including the occasional migrant), but over half of the observed kills were warthog and Cape buffalo.

During three 96-h watches, the females moved 20–40 km from their usual territories and reached the migratory herds. Observations made before the lions came to within 1 km of the migratory herds contribute to the data on prey scarcity, whereas the subsequent hours of observation contribute to the data on prey abundance.

Data on grouping patterns are based on more than 1,500 sightings of radio-collared females from July 1984 to December 1987. All other observations might be biased by differential visibility of different-sized groups. Observations of females in estrus were excluded from analysis because they are sequestered by a consorting male (Schaller 1972; Packer and Pusey 1982) and hence are unable to associate freely. Observations of the same female include only sightings that were made at least 5 d apart, because data separated by this period of time were found to be statistically independent. Data from all prides of the same size have been pooled because there was no significant heterogeneity among prides.

<center>RESULTS AND DISCUSSION</center>

<center>*Group-Size-Specific Food-Intake Rates*</center>

During the season of prey abundance, neither the average nor the variance of per capita daily food-intake rate varied significantly across group sizes (fig. 1). However, during prey scarcity, both the average and variance were significantly lower for females in groups of two to four females than for lone females or for groups of five to seven females. Indeed, pairs of females did not feed in 170 h of observation during prey scarcity. Solitary females did not differ from females in groups of five to seven in either the average rate or the variance. The average and
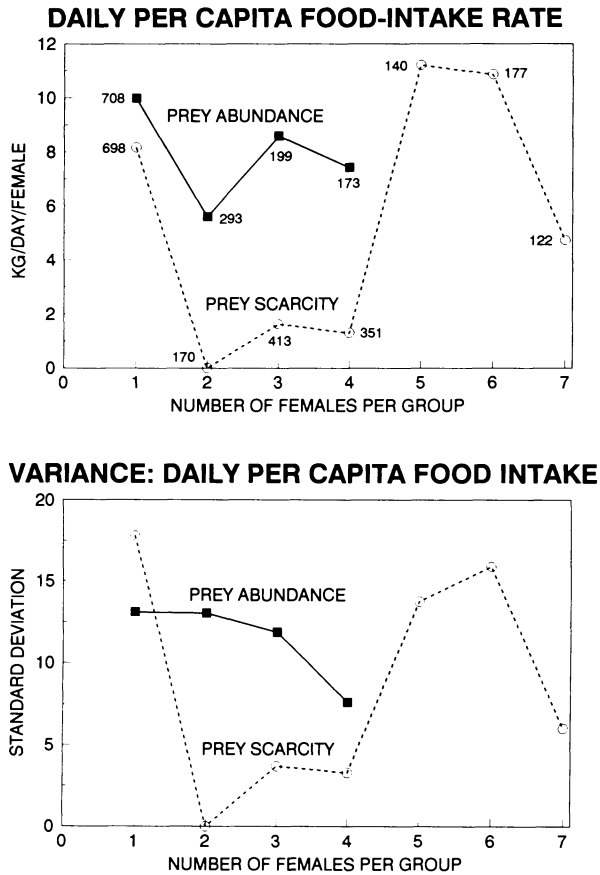
DAILY PER CAPITA FOOD-INTAKE RATE

VARIANCE: DAILY PER CAPITA FOOD INTAKE

Fig. 1.—Daily per capita food consumption for each group size during periods of prey scarcity and prey abundance. *Top,* Mean consumption rate. Number of hours of observation are indicated for each group size. The number of independent observations for some group sizes was so small that adjacent group sizes were combined for statistical tests: prey scarcity, two to three and five to seven; prey abundance, four to five. Results are unchanged if prey-scarcity data for groups of seven are excluded. Prey scarcity: Kruskal-Wallis test, $H = 11.59$, df = 3, $n = 27$, $P < .01$; Mann-Whitney U-test, 1 vs. 2–4, $U = 20.5$, $n_1 = 9$, $n_2 = 13$, $P < .02$; 2–4 vs. 5–7, $U = 2$, $n_1 = 13$, $n_2 = 5$, $P < .002$; 1 vs. 5–7, $U = 18$, $n_1 = 9$, $n_2 = 5$, NS. Prey abundance: $H = 2.35$, $n = 23$, NS. *Bottom,* Standard deviation treated statistically as above. Prey scarcity: squared-ranks test, $T_2 = 14.07$, df = 3, $P < .01$; 1 vs. 2–4, $T_1 = 2.67$, $P < .01$; 2–4 vs. 5–7, $T_1 = 2.68$, $P < .01$; 1 vs. 5–7, $T_1 = 1.26$, NS. Prey abundance: $T_2 = 0.67$, df = 3, NS.

the variance of food intake of lone females or females in groups of five to seven did not differ between times of prey abundance and prey scarcity; but during prey scarcity, females in groups of two to four had a lower average (Mann-Whitney U-test, $U = 27$, $n_1 = 12$, $n_2 = 13$, $P < .02$) and a lower variance (squared-ranks test, $T_1 = 3.11$, $P < .01$). Thus, only females in groups of two to four risked nutritional stress when prey was scarce.

The variation in food-intake rate during prey scarcity resulted largely from differences in meal size. There was significant variation across group sizes both in per capita meal size (Kruskal-Wallis, $H = 6.68$, $n = 37$, $P < .05$) and in the amount of meat consumed by the entire group of females ($H = 7.69$, $P < .05$). Solitary females acquired as much food as did groups of two to four females, but because they did not have to divide it with companions, they gained larger meals than females in groups of two to four (U-test, $U = 30$, $n_1 = 12$, $n_2 = 12$, $P < .02$). Groups of five to seven females procured much larger carcasses than either solitaries ($U = 38$, $n_1 = 13$, $n_2 = 12$, $P < .05$) or groups of two to four ($U = 32$, $P < .02$) and consequently gained per capita meal sizes similar to those of solitaries and larger meals than individuals in groups of two to four ($U = 44$, $.10 > P > .05$).

Competition between groups of females for individual carcasses was rare (see below) as were losses of meat to hyenas. Groups of five to seven females gained large carcasses in two ways. First, they gained all of their meals from predation ($n = 12$), whereas groups of one to four females acquired 62.5% of their meals by scavenging (Fisher test, $n = 24$, $P < .05$). Second, large groups frequently captured Cape buffalo. Buffalo are an important component of the diet during periods of prey scarcity but are almost never tackled by small groups of females in the Serengeti. Warthog were the most frequent prey of small groups.

During prey abundance, meal size and group size were not related for either meal size per individual or per group, and the lions fed exclusively on wildebeest, zebra, and Thomson's gazelle.

Our results contrast with earlier analyses for a number of reasons. First, Schaller's (1972) data on foraging efficiency were restricted to hunting success. These could not be used to estimate *daily* feeding rates since there was no way to estimate daily hunting *frequency* (Packer 1986). Moreover, by concentrating on hunting success, earlier studies neglected the importance of scavenging. Schaller (1972) emphasized that lions frequently scavenged, and over 40% of carcasses in our study were acquired by scavenging ($n = 79$).

Second, previous analyses focused exclusively on the feeding efficiency of lions while hunting the three most common migratory species, Thomson's gazelle, wildebeest, and zebra. However, food was clearly not limiting when these species were abundant (see the Methods section). When food was scarce, the lions' primary prey were warthog and buffalo, species for which no previous data were available.

Finally, it has been suggested (Packer 1986) that a single female would be unable to use an entire carcass because of the high probability of scavenging by other lions. Consequently, solo foragers would be expected to gain only the same food-intake rates as females in any other group size (Fretwell and Lucas 1970). We found that solo females did lose meat to conspecifics, but these losses were so rare that solitaries nevertheless had food-intake rates higher than those of moderate-sized groups when prey was limiting (fig. 1).

Predicted Grouping Patterns

Previous analyses attempted to determine the optimal group size for lions hunting particular prey species, Thomson's gazelle, wildebeest, or zebra. How-

ever, when food was limiting, the lions typically hunted several different species each day, and the choice of prey was highly opportunistic. Nevertheless, the lions' grouping patterns were stable during our observations; on the average, foraging groups changed size only once every 48 h during prey abundance and once every 75 h during prey scarcity. None of the 42 changes was obviously related to hunting. The major contexts for change were (1) scattering in response to encounters with extra-pride males or females (16.7%), (2) temporary separation by lactating mothers to tend to their immobile and isolated young (16.7%), (3) aggregation at a carcass by pride mates (19%), and (4) separation from companions after feeding (usually moving to a water hole for a drink) (19%). Hence, the lions did not adjust their group sizes according to the species of potential prey, as assumed previously.

Therefore, we have examined the grouping patterns of female lions according to prey availability because these conditions persist over several consecutive months. The predicted grouping patterns during each season are based on the data in figure 1. Note, however, that no preferred group size can be predicted for the season of prey abundance because the feeding efficiencies of all group sizes are statistically indistinguishable at that time of year. Similarly, during prey scarcity, differences in mean and variance among groups of one, five, and six are not significant.

Following Caraco and Wolf's (1975) original model, the group sizes that maximize food intake are simply those with the highest per capita daily average. During prey scarcity, females should forage alone or in groups of five or six females. In order to find the optimal group size from a risk-sensitive model, it is necessary to estimate a female's daily requirement (Caraco et al. 1980). One estimate of this requirement (R) can be based on the average food intake of females during prey abundance. Per capita food intake is similar across group sizes during prey abundance and averages 8.5 kg per female per day. However, females may increase their food intake at these times in anticipation of prolonged food deprivation during prey scarcity (see Katz 1974). As an alternative, we also use Schaller's (1972) estimate of $R = 5.0$ kg per female per day. According to a static stochastic model (Stephens and Charnov 1982), females are again predicted to forage alone or in groups of five or six during prey scarcity. These group sizes minimize Z scores regardless of whether $R = 8.5$ or $R = 5.0$.

These group sizes are also optimal according to a dynamic model (Clark 1987; Houston et al. 1988) that incorporates the data in figure 1. The state variable in Clark's model is stomach contents; and the dynamic model finds the group size that minimizes the risk of starvation over 30 d. Clark assumed that a lion's maximum stomach capacity is 30 kg, that its daily requirement is 6 kg, and that the lion dies once its stomach is empty. Our observations suggest that the maximum is closer to 50 kg, and we estimate that the daily requirement (R) is 5.0–8.5 kg. Although Clark's model greatly exaggerates the risks of starvation (Smuts 1979), we cannot estimate the actual risks (see below). We have therefore modified the first two assumptions and kept the third assumption unchanged. We have found the optimal group sizes solely to provide a comparison with the Z-scores model. After substituting our daily food-intake data for each group size, the dynamic model gives the same results as the static model for each day after 6–10 d.

Because solitaries do as well as groups of five or six females, the optimal group sizes are stable and are not expected to vary with kinship (Giraldeau 1988). Thus, remarkably, all foraging models make the same predictions: during prey scarcity, females should forage alone or in groups of five or six females.

Do Females Forage in Group Sizes That Maximize Foraging Efficiency?

Lion social organization places important constraints on female grouping patterns. Females associate peacefully only with members of their own pride, and prides are formed by the division of preexisting kin groups (Hanby and Bygott 1987; Pusey and Packer 1987). Adult females in our study populations never form prides with non-kin (Packer 1986; Pusey and Packer 1987). Hence, pride size sets an upper limit on group size. Therefore, if grouping is related to foraging efficiency, females in prides of two to four females should forage alone during prey scarcity, whereas females in prides of five or more should forage either alone or in groups of five or six females. Although the performance of females in groups of eight or more is unknown, it is unlikely to exceed that of groups of five or six: buffalo are the largest prey in the Serengeti.

Figure 2A shows that, during prey scarcity, the radio-collared females in prides of 2–4 females formed groups that deviate strikingly from these predictions. Rather than forage alone, females in these pride sizes most frequently foraged in the maximum possible group size (e.g., prides of 2 females foraged in groups of 2 females, prides of 3 in groups of 3, etc.). In contrast, figure 2B shows that, as would be expected from the foraging data, females in larger prides most commonly foraged in intermediate group sizes. Females in prides of 5, 7, and 11 all foraged most frequently in groups of 5 or 4, and those in prides of 6 showed a nonsignificant tendency to forage in groups of 5.

Although the results from large prides are close to the predicted group sizes of 5 or 6, the foraging data suggest that groups of 4 females do poorly compared with groups of 5, and yet the pride of 11 clearly preferred to form groups of 4. However, this is the only pride that did not contribute to the data in figure 1. Although several adjacent prides were sampled in similar habitat (and showed similar prey composition and distribution), we cannot exclude the possibility that some quirk in local conditions might have favored foraging in groups of 4 for the pride of 11.

Group size did not significantly affect per capita food intake during prey abundance, and thus no specific grouping pattern would be predicted. Figure 3 shows that females in all pride sizes were more likely to be found alone during prey abundance than during prey scarcity (Wilcoxon test, $T = 5$, $n = 9$ pride sizes, $P < .05$), but in other respects, the grouping patterns were similar: small prides tended to be found in the maximum group size, and large prides in an intermediate group size. These findings are discussed more fully in the following subsection.

Our grouping data cannot be compared with previous analyses of Schaller's (1972) data. His observations were collected on lions that were not radio-collared, the data were not separated according to sex or social-group size, and most analyses of his data have been based on mean group size. Grouping patterns must measure the choices of individuals rather than groups (Jarman 1974; Clutton-

SEASON OF PREY SCARCITY
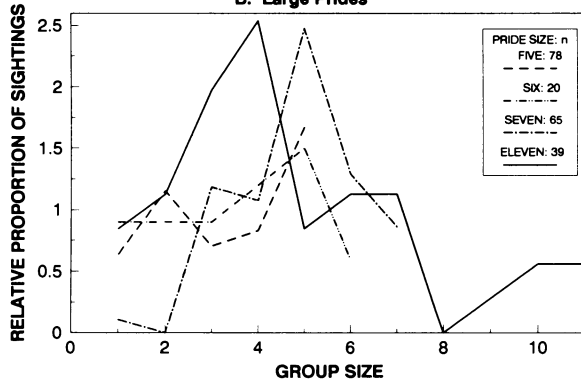### A. Small Prides
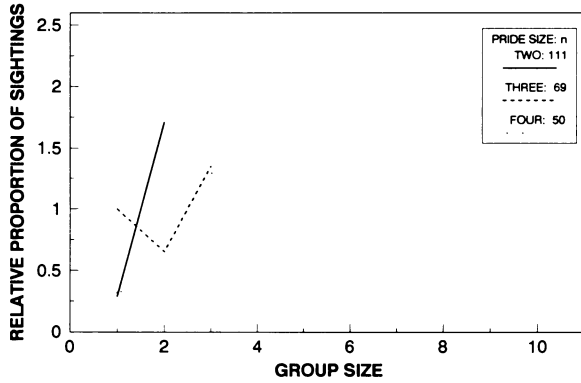
B. Large Prides

FIG. 2.—Relative proportion of sightings during prey scarcity in which radio-collared females were found in groups of each size for A, prides of 2–4 females; B, prides of 5–11 females. Pride size is marked at the beginning and end of each distribution. The relative proportion is the observed number of sightings of each group size multiplied by x/n, where x is the pride size (the number of possible group sizes for that size pride) and n is the total number of sightings of that size pride. Thus, females found equally often in each group size would have a relative proportion of 1.0 for each, regardless of pride size. Data are plotted only for those pride sizes for which $n > 3x$, and statistics are based on the untransformed data. The null hypothesis for all tests is that females spent equal time in each possible group size. Females in the following pride sizes showed heterogeneous (G-test, $P < .05$) grouping patterns: 2, 4, 5, 7, 11. Females in prides of 2, 4, and 7 spent less time alone than expected (binomial test, $P < .05$). Females in prides of 2, 3, 4, and 5 all spent significantly more time than expected in the maximum pride size. The only other significant positive deviations were for females in prides of 7 to be in groups of 5 and prides of 11 to be in groups of 4.
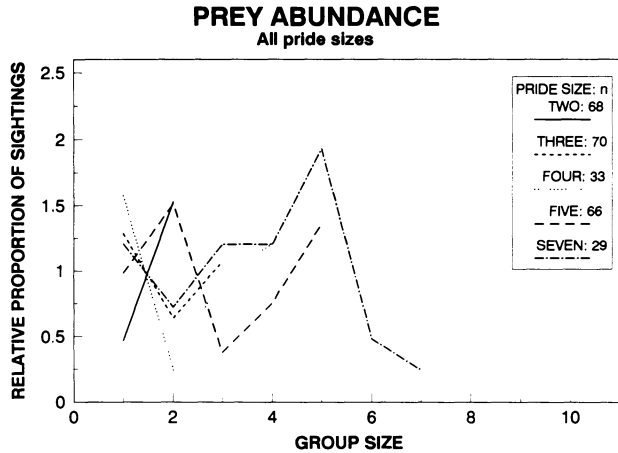
FIG. 3.—Relative proportion of sightings during prey abundance in which radio-collared females in all pride sizes were found in groups of each size. Conventions as in fig. 2. Females in prides of two, four, and five showed uneven (G-test, $P < .05$) grouping patterns. Females in prides of two spent less time alone and more time than expected in the maximum pride size (binomial test, $P < .05$).

Brock and Harvey 1984), and it is clearly inappropriate to define the preferred group size as the mean when the optimal group size is either a maximum or a minimum or when there are two maxima.

Factors Influencing Lion Grouping Patterns

The grouping patterns illustrated in figure 2 provide only weak support for predictions based solely on foraging efficiency. The following three factors appear to override the effects of group-size-specific foraging success.

1. *Cooperative cub defense.*—Infanticide by incoming males accounts for 27% of cub mortality (Bertram 1975; Packer and Pusey 1983*a;* Packer et al. 1988). When new males first enter a pride, they kill all of the small cubs and evict the older cubs and subadults (Hanby and Bygott 1987; Pusey and Packer 1987). Consequently, all females in the pride resume mating and give birth at about the same time (Packer and Pusey 1983*b*). Female pride mates with cubs of a similar age pool them together when the cubs are 4–6 wk old to form a highly stable "crèche" (Packer and Pusey 1983*a;* Packer 1986; Cairns 1990). These crèches persist until the cubs are about 1.5–2 yr old, at which point the mothers resume mating (Pusey and Packer 1987). Mothers are almost always found together when their cubs are 30–600 d old (fig. 4).

We have no evidence that a crèche provides nutritional advantages to cubs. Similar to figure 1, an analysis of female belly size suggested that mothers in crèches involving three or four females suffer lower mean food intake than those involving one or two females (Packer 1986; note, however, that this did not control for prey availability). Communal rearing is expected to reduce the interval between meals if the young do not always accompany their mothers and if

ASSOCIATIONS OF MOTHERS
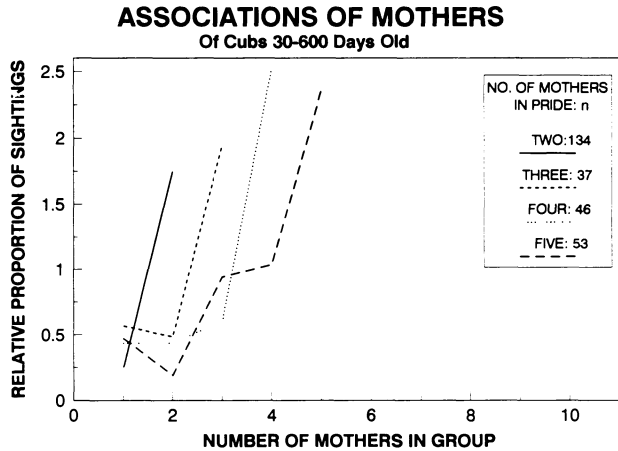### Of Cubs 30-600 Days Old

FIG. 4.—Relative proportion of sightings in which mothers were found in maternity groups of each size. Relative proportion calculated as in fig. 2, but here x is the number of mothers in the same pride with cubs aged 30–600 d at the same time. The tendency for all mothers to be together was highly significant ($P < .001$), regardless of the number of mothers in the pride. Data from all times of year are combined because there was no effect of prey availability on crèche gregariousness.

TABLE 1

EFFECTIVENESS OF GROUP DEFENSE AGAINST
INFANTICIDAL MALES

| | AGGRESSIVE ENCOUNTERS BETWEEN FEMALES AND EXTRA-PRIDE MALES | |
NO. OF DEFENDING FEMALES	Some Cubs Survive	All Cubs Die
≥2	5	0
1	1	5

NOTE.—Data were collected from 1978 to 1988. Note that no defending males were present in any of these encounters. Fisher test, $P < .05$.

mothers forage independently of each other (Caraco and Brown 1986). However, lactating mothers typically forage together and return synchronously to nurse their cubs. As the cubs grow older, they remain near their mothers during the hunt.

Instead of providing nutritional advantages, the function of a crèche appears to be defense. Mothers defend their cubs against nomadic males (see Packer and Pusey 1983a, 1984), and table 1 shows that groups of defending females are more effective than solitary mothers. In addition, females in prides of two to seven females suffer significantly lower rates of male takeovers (and hence infanticide) than do solitary females (Packer et al. 1988).

PREY SCARCITY, NO CRECHE IN PRIDE

A. Small Prides
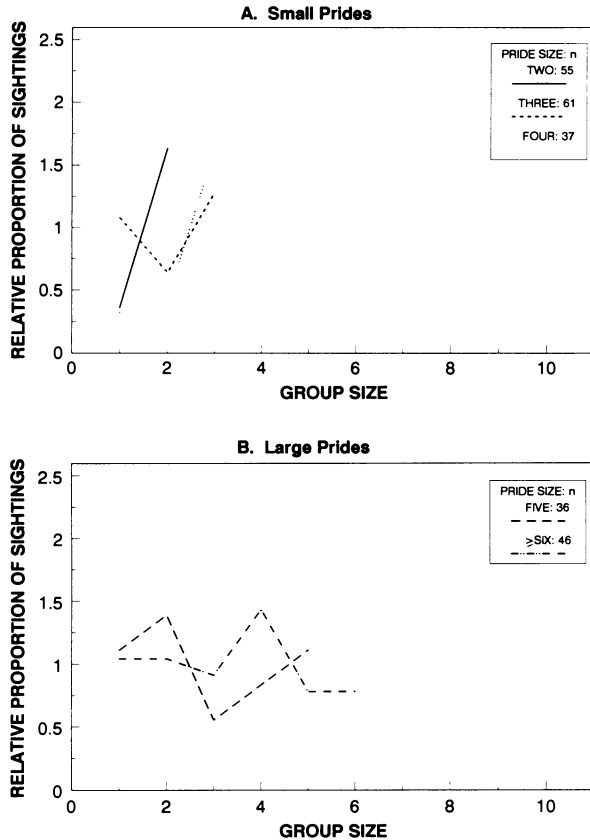

B. Large Prides

Fig. 5.—Relative proportion of sightings during prey scarcity in which radio-collared females were found in groups of each size (excluding data from prides when they contained a crèche) for A, prides of 2–4 females; B, prides of 5–11 females. Data from prides of 6 or more have been lumped. Conventions as in fig. 2. Females in prides of 2 and 4 showed heterogeneous (G-test, $P < .05$) grouping patterns. Females in prides of 2 and 4 spent less time alone and more time than expected in the maximum group size (binomial test, $P < .05$). Females in prides of 5 or more showed no significant tendency to form groups of any particular size.

Crèche formation clearly contributed to the grouping patterns of the large prides. Every pride of five or more females contained a crèche some time during the study, and 69% of these crèches involved four or five mothers ($n = 13$ groups). After excluding data from each pride when it contained two or more mothers with dependent cubs, large prides showed no tendency to form any particular group size during prey scarcity (fig. 5B).

However, group-size-specific foraging efficiency during prey scarcity might limit the number of females that can successfully operate as a crèche. Crèches involving up to nine mothers have been observed; but the cubs in these extremely large communal litters often appear undernourished. It is therefore possible that feeding efficiency limits cub survival and hence the number of mothers in large

prides. Alternatively, the number of mothers involved in a crèche may be merely a by-product of the reproductive rates of females. A clear distinction between these alternatives might be made by comparable studies elsewhere. Lions feed on radically different types of prey in different parts of Africa (Schaller 1972; Packer 1986; Prins and Iason 1989) and have different reproductive rates (Van Orsdol et al. 1985). It is therefore unlikely that an optimal foraging-group size would always coincide with the typical number of mothers involved in a crèche.

Although females in prides of two to four did not forage in the group size that maximized feeding efficiency and instead foraged in as large a group as possible, cub defense by itself is inadequate to explain their extreme gregariousness. Only 25% of crèches in prides of three or four females (n = 8 crèches) involved all the females in the pride, and only half of the prides of two had maternity pairs (n = 6 prides). After excluding data from each pride when it contained two or more mothers with dependent cubs, most small prides still formed as large a group as possible (fig. 5A).

2. *Group territoriality.*—The large group sizes of small prides appeared to be a direct response to the hazards of encountering larger prides. During prey scarcity, females in all pride sizes periodically left their territories in search of food, and they typically moved as a unit. Consequently, females encountered other prides both outside and within their own territories and were vulnerable to potentially fatal attack by larger prides (see Schaller 1972; Packer et al. 1988). Inter-pride encounters between females occurred on an average of once every 116 h during this study. Over half of these encounters (17 of 30) ended with an intense chase. The larger group won 13 of 15 encounters in which the composition of both groups was known (sign test, P < .01).

Small prides would be most likely to encounter large prides in groups of four or five (fig. 2), and it would therefore be safest for a small pride to form as large a group as possible (Hamilton 1971; Alexander 1974; Wilson 1975). Although solitary females gained adequate food during prey scarcity, they were particularly vulnerable to attack by groups. This may contribute to the significantly higher mortality rates of solitary females (reported in Packer et al. 1988).

The importance of inter-pride competition to female fitness is only now becoming apparent. Four prides of one or two females have recently lost their territories to larger neighboring prides; and successful breeding appears to be impossible without a territory. Females that were forced to leave their territories by extreme prey scarcity returned to them almost immediately after feeding successfully elsewhere. Intergroup competition is primarily over land rather than over specific carcasses (Packer 1986). Female pride mates do not cooperate in defending a carcass against females from other prides. If females from different prides meet at a carcass containing a significant amount of meat, then the two prides feed together. During this study, 27% of the inter-pride encounters between females (n = 30) occurred at a carcass. In half of these (four of eight), both prides fed from the same carcass; chases near a carcass (n = 5) occurred only after most of the carcass had been consumed. Thus, although a specific food item is sometimes contested, the long-term value of an area (see Davies and Houston 1984) appears to be the primary goal of territorial defense.

3. *Female reproductive patterns.*—After we excluded data from each pride

PREY ABUNDANCE, NO CRECHE IN PRIDE
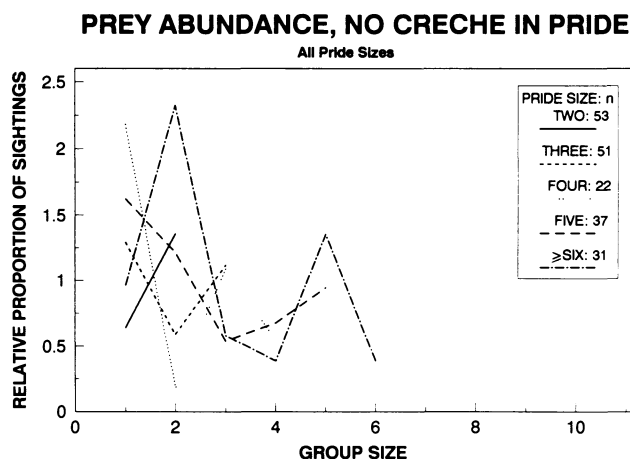### All Pride Sizes

FIG. 6.—Relative proportion of sightings during prey abundance in which radio-collared females in all pride sizes were found in groups of each size, excluding data from prides when they contained a crèche. Conventions as in fig. 2. Females in prides of two, four, and six showed heterogeneous (G-test, $P < .05$) grouping patterns. Females in prides of two spent more time together than expected, whereas females in prides of four spent significantly more time alone (binomial test, $P < .05$). The only other significant deviation is for females in prides of six or more to be in pairs.

when it contained two or more mothers with dependent cubs, females were found in smaller groups during the season of prey abundance than during prey scarcity (Wilcoxon test, $T = 6$, $n = 9$ pride sizes, $P < .05$; figs. 5, 6). The lower levels of gregariousness during prey abundance resulted at least partly from seasonal reproduction during this study.

First, collared females were in estrus more often during prey abundance ($T = 29.5$, $n = 16$ females, $P < .05$). Estrous females were more frequently away from their female pride mates (Wilcoxon test, $T = 7$, $n = 13$ females, $P < .01$) because their movements were restricted by their consort partner (see the Methods section). Although sightings of collared females in estrus were excluded from figures 2–6, their companions experienced a similar seasonal increase, and consequently, the pride split up more often during prey abundance. Seasonal reproduction may in part have been due to improved nutrition resulting from the return of the migratory herds (see Schaller 1972; Rudnai 1973) and also due to the seasonality of male takeovers (48% of takeovers occurred in November and December during the years of this study; G-test, $G = 13.28$, df = 5, $n = 25$, $P < .05$). Nomadic males follow the migratory herds that return to the study area at the onset of the rains in November. Infanticide of small cubs and eviction of older cubs by the incoming males causes most females to come into estrus within a few days of the takeover (Packer and Pusey 1983b, 1984).

Second, births were seasonal, with 76% of the births by radio-collared females occurring between March and July ($G = 17.31$, df = 5, $n = 33$, $P < .01$). A female becomes secretive during pregnancy, keeps her cubs hidden in thick vegetation until they are at least 1 mo old (during which time they are immobile and

vulnerable to numerous other predatory species), and then brings them out to join the other cubs in the pride (Schaller 1972; Rudnai 1973). Consequently, more solitary foraging occurred during pregnancy and the first 30 d of lactation than at other times during cub rearing ($T = 20.5$, $n = 14$ females, $P < .05$). Because of seasonal reproduction, most pregnancies or early lactation occurred during prey abundance, whereas the later, more gregarious stages of cub rearing occurred during prey scarcity ($T = 18.5$, $P < .05$).

CONCLUSIONS

Group-size-specific foraging efficiency is insufficient to account for lion grouping patterns. If foraging efficiency were the only factor affecting grouping, female lions should have remained either alone or in a group of five or six females during periods of prey scarcity. Prides containing five or more females most commonly foraged in groups of four or five females during prey scarcity. Although these sizes were close to the size that maximized feeding efficiency, they were entirely the result of the formation of defensive maternity groups. In the absence of a crèche, females in these prides showed no tendency to form a foraging group of any particular size. Nevertheless, mothers in large prides may follow a rule of thumb that consists of remaining in constant association with the other mothers in the pride. Formation of a crèche would often ensure that a mother foraged in a group size close to a foraging optimum (although it would guarantee a suboptimal foraging-group size in a small pride). Whether foraging efficiency has any effect whatsoever on the grouping preferences of large prides could best be clarified by the collection of comparable data from lions in a different part of Africa. The group-size-specific foraging success of lions in areas with entirely different herbivore assemblages is unlikely to be the same as for lions in the Serengeti; typical crèche size would also be expected to vary.

Females in prides smaller than five remained in the largest possible group size rather than following the optimal-foraging strategy of foraging alone during prey scarcity. This grouping pattern was not entirely the result of crèche formation. The extreme gregariousness of small prides probably resulted from the risk of encountering groups of four or five females from larger prides and from the need to defend territory against larger neighboring prides.

Although we have demonstrated that cub defense, group territoriality, and female reproductive patterns all influence lion grouping patterns, we cannot weigh their effects against the costs and benefits of group foraging. Ideally, such data could be incorporated into a comprehensive dynamic model (e.g., Mangel and Clark 1988). Unfortunately, our direct observations of cub defense (table 1) are inadequate to estimate the optimal crèche size, and it would be difficult to estimate the precise group-size-specific effects of group territoriality.

Most importantly, the precise effects of prolonged food deprivation cannot be measured in wild lions. Clark's (1987) dynamic model assumed that a lion dies as soon as its stomach is empty. In fact, female lions in the Serengeti can survive for several weeks on an empty stomach and may endure far longer periods each year without meeting their daily requirement.

Lions may be able to disregard the optimal *foraging*-group sizes for extended periods because feeding efficiency is relatively unimportant in such a large, mobile animal (for a discussion of the allometry of fasting ability, see Lindstedt and Boyce 1985). Being able to withstand relatively long periods of food deprivation, female lions might maintain condition by foraging alone only occasionally, and figures 2 and 5 show that females in all pride sizes spent at least some time alone during prey scarcity. Moreover, when they are close to starvation, Serengeti lions can always trek to the migratory herds. During prey scarcity, we followed groups of one to four females on extraterritorial forays of up to 40 km to the migratory herds (see the Methods section). The prides then quickly returned home after a succession of large meals. Thus, it is plausible that short-term disadvantages of group foraging are generally overridden by long-term advantages of grouping.

We are able to measure the overall effect of pride size on female fitness. Females are classified as adult after they have reached 4 yr, by which time they have started breeding (Packer et al. 1988). Pride size varies from 1 to 18 adult females. Adult females in prides of 3–10 gain the highest per capita reproductive success, and those in prides of 3 or more have the lowest mortality rates (Packer et al. 1988). Female dispersal patterns are such that most adult females live in prides of 2–9 females (Pusey and Packer 1987). Thus, females are sensitive to the long-term payoffs conferred by specific pride sizes, and most adult females live in prides in the optimal size range.

Female lions are the only female felids to live in social groups, and this may ultimately be explained by their group territoriality. Sociality in lions has traditionally been attributed to the advantages of group hunting, but most studies show that solitary females have feeding success comparable to groups (for a review, see Packer 1986). This study indicates that large prey size is indeed a permissive factor allowing individuals to forage together, but other factors provide the positive advantages of living in groups: there is never a nutritional disadvantage of foraging solitarily, and groups of five or six females are able to feed as well as solitaries only because of their ability to acquire larger carcasses during prey scarcity. Cub defense is one advantage of grouping in lions, but it is insufficient to explain the distribution of female sociality since infanticide is found in many solitary cat species (Packer and Pusey 1984). Several unique characteristics of lion ecology may have favored group territoriality (Packer 1986). First, lions live at higher densities than any of the other large cats, and high population density can lead to the shared defense of a common territory (Davies and Houston 1981; Brown 1982, 1987). Second, the relatively large size of the lions' prey may result in a pattern of resource renewal that permits group foraging in a common territory (Waser 1981; Davies and Houston 1984). An analysis of group territoriality in lions will be presented elsewhere (Packer and Pusey, unpublished manuscript).

We stress that we do not disagree with the major theoretical developments of earlier workers. The questions of rate maximization, risk sensitivity, inclusive fitness, and stability should all be considered when investigating grouping patterns. However, we do believe that these effects will be most apparent in a species that forms groups solely for the purposes of foraging. Female lions have many other problems to solve besides catching their next meal.

SUMMARY

Extensive observations of foraging female lions reveal that two group sizes maximize foraging success during the season of prey scarcity: one female and five or six females. Foraging success does not vary significantly with group size when prey is abundant. Female lions live in fission-fusion social units (prides) and forage only with members of their own pride. If lion grouping patterns were primarily related to group-size-specific feeding efficiency, females in prides containing fewer than five females should forage alone when prey is scarce, whereas females in larger prides should forage alone or in groups of five or six. However, extensive data on the grouping patterns of radio-collared females show that females in small prides most commonly forage in as large a group as possible, even at the expense of foraging efficiency. Females in large prides most often forage in intermediate group sizes of four or five. However, mothers keep their cubs in a crèche and form highly stable maternity groups that are effective in defending the cubs against infanticidal males. Most large prides contain a crèche involving four or five mothers, and in the absence of a crèche, large prides show no preference for any group size. Females also compete aggressively against neighboring prides, and larger groups successfully repel smaller ones in territorial disputes. Small prides appear to be excessively gregarious in order to compete against larger neighboring prides.

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