

Non-offspring nursing in social carnivores: minimizing the costs

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We compare the nursing behavior of two species, African lions (*Panthera leo*) and spotted hyenas (*Crocuta crocuta*), and show that non-offspring nursing is much less common in hyenas than lions. Hyenas spend less time with their cubs, are more alert during the suckling attempts of cubs, and more frequently resist the attempts of non-offspring. Vigilance against milk theft may therefore influence the distribution of non-offspring nursing across species. Our detailed study of non-offspring nursing in lions shows that females preferentially nurse their own offspring and that cubs are more surreptitious when attempting to suckle from other females. Non-offspring nursing in lions is most common when the costs are lowest. First, non-offspring nursing is more common among close kin. Second, females with small litters, and presumably more milk to spare, give a higher proportion of their nursing to non-offspring. Third, females give a higher proportion of their nursing to non-offspring as their own cubs grow older and need less milk. Cubs reared in crèches do not appear to gain more milk than cubs raised alone, and females do not show any evidence of reciprocity in nursing one another's offspring. We suggest that non-offspring nursing in lions occurs as a by-product of the females' communal defense of their cubs against infanticide. *Key words*: cooperation, kin selection, lions, non-offspring nursing, parental care, reciprocity, spotted hyenas. [*Behav Ecol* 5:362–374 (1994)]

Lactation imposes high metabolic costs (Hanwell and Peaker, 1977) and can significantly increase the mortality rates of female mammals (Clutton-Brock et al., 1989). We would therefore expect females to distribute their milk exclusively to their own offspring. Nevertheless, extensive non-offspring nursing has been described in a wide variety of species (Packer et al., 1992). Although non-offspring nursing has usually been assumed to confer an array of mutualistic or inclusive fitness advantages (e.g., Bertram, 1976; Riedman, 1982; Wilkinson, 1992), it can also result from parasitism of unwilling females (e.g., McCracken, 1984; Reiter et al., 1978), but few studies have been sufficiently detailed to distinguish between these alternatives.

There are at least two ways in which females could gain immediate benefits from rearing their young communally and nursing non-offspring. First, in some laboratory rodents, non-offspring nursing leads to the more rapid growth of all young, apparently because the increased stimulus of suckling results in the production of more milk by all females (König, 1993; Menella et al., 1990; Saylor and Salmon, 1969, 1971). However, although captive females can compensate for increased milk production by increasing their food intake from an ad libitum diet, this option is not available to wild mammals with limited food availability (e.g., Loudon and Kay, 1984). Second, non-offspring nursing may reduce variance in food intake if the behavior is reciprocated by other mothers (Caraco and Brown, 1986). If individual mothers spend long periods away from their young, or show temporal variation in their foraging success, reciprocal non-offspring nursing could shorten the interval be-

tween meals and provide a more constant, if not more plentiful, supply of milk to each offspring.

Alternatively, females may often be constrained to rear their young together for non-nutritional reasons, and non-offspring nursing then occurs as an unavoidable consequence of proximity to the young of other females. In such cases, the extent of non-offspring nursing will depend on a trade-off between the costs of losing milk to parasitic non-offspring, and the costs of prevention. The ability of females to prevent non-offspring nursing is known to vary between species. For example, female Mexican free-tailed bats leave their young in caves containing millions of pups and are beset by suckling attempts from non-offspring as they return to their own young, yet they manage to reject most of these attempts and prevent the loss of all but a small amount of milk to non-relatives (McCracken, 1984). Female elephant seals give birth on crowded beaches and sleep beside their pups. Although they will attack any non-offspring that tries to suckle from them, they do not always detect the theft and so lose a significant amount of milk (Reiter et al., 1978). Finally, female house mice benefit from sharing nests through improved nest defense but nurse all young indiscriminately, probably because of the difficulties of distinguishing and rejecting non-offspring (Manning et al., in press).

The costs of losing milk to non-offspring will be influenced by several factors. First, across taxa, non-offspring nursing increases in frequency and is better tolerated in species with larger litters (Packer et al., 1992). Packer et al. argued that females adapted to raising litters of several offspring (polytocous species) will suffer lower costs from non-

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offspring nursing than females adapted to raising a single offspring (monotocous species) because the milk given to each polytocous young is a smaller proportion of the total. A polytocous female that loses some of her offspring during a temporary food shortage might easily produce sufficient milk for her own and other young once conditions improve. Therefore, within polytocous species, we should expect females with smaller than average litters to show more non-offspring nursing than females with larger litters. Second, offspring age should affect the costs of non-offspring nursing, with females attempting to nurse their own young most exclusively when the demand from their own offspring is greatest. This may not be possible, however, if females are unable to prevent larger non-offspring from supplanting their own young from their teats (e.g., Menella et al., 1990). Third, food availability will influence the milk supply of females and hence the costs of nursing non-offspring. The comparative study by Packer et al. (1992) revealed that non-offspring nursing is most common in captivity, when food is most abundant. It has even been suggested that well-fed female bats should dump excess milk by nursing non-offspring to decrease their weight for the next foraging trip, maintain milk production, and prevent infection (Wilkinson, 1992).

There are several evolutionary advantages of non-offspring nursing that can offset the costs of milk loss. First, if the recipients are close kin, the costs will be ameliorated by inclusive fitness effects (Hamilton, 1964). Packer et al. (1992) found that non-offspring nursing was most common in polytocous species where female group sizes were small, and average kinship therefore highest. Second, females may directly enhance their fitness by improving the survival of individuals that eventually help them or their offspring through better thermoregulation (Sayler and Salmon, 1969), cooperation (Bertram, 1976), or dilution effect (Hoogland et al., 1989; Wilkinson, 1992).

In this article, we compare the nursing behavior of two social carnivores: African lions, in which females form crèches and non-offspring nursing is ubiquitous (Bertram, 1976; Schaller, 1972), and spotted hyenas, in which non-offspring nursing is very rare (Holekamp and Smale, 1990; Kruuk, 1972; Mills, 1985). We then examine in detail the patterns of non-offspring nursing in lions. We test whether females raising cubs in crèches nurse more than singleton mothers. Then we test whether female lions discriminate between cubs, evaluate the hypotheses that non-offspring nursing is influenced by kinship, litter size, cub age, and food availability, and test for evidence of reciprocity. Finally, we discuss whether female lions rear their cubs together because of positive advantages of non-offspring nursing or because they are constrained to do so for other reasons.

Biology of study species

Lions

Lions of the Serengeti ecosystem and Ngorongoro Crater live in permanent social groups, called prides, which are fission-fusion units consisting of 1–18 adult females, their dependent offspring and a coalition of 1–9 adult males (Packer et al., 1988). All

the females are relatives and were either born in that pride or formed the pride with female members of their natal cohort; the adult males entered the pride from elsewhere (Pusey and Packer, 1987). Coalitions of males compete intensely for residence in prides. Coalitions usually consist of relatives from the same pride and male reproductive success increases with coalition size (Bygott et al., 1979; Packer and Pusey, 1982; Packer et al., 1988, 1991a). Every two years, on average, a pride is taken over by a new coalition of males that completely replaces the resident coalition, evicts the subadult males and females, and kills all the dependent cubs (Bygott et al., 1979; Packer and Pusey, 1983a; Pusey and Packer, 1987). As a result, the adult females subsequently breed synchronously and often give birth to synchronous cohorts of cubs (Packer and Pusey, 1983b).

Female lions breed at any time of year. They have four teats, and more than 98% of litters contain 1–4 cubs (Packer and Pusey, 1987). Mothers keep their cubs hidden for about six weeks, then form a highly stable crèche with the other mothers in the pride (Cairns, 1990; Packer, 1986; Packer and Pusey, 1983a; Packer et al., 1990). Subsequently, the mothers are almost always found together, and associate much more frequently than females without cubs (Packer et al., 1990; Pusey and Packer, 1994). Cubs are weaned at 6–8 months but remain with their mothers until they are at least 18 months old (Packer and Pusey, 1983b; Schaller, 1972).

Hyenas

Spotted hyenas in the Serengeti ecosystem and Ngorongoro Crater live in clans of about 60 individuals (Frank, 1986a; Holekamp and Smale, 1990; Kruuk, 1972). Females remain in their natal clan, and all breeding males enter the clan from elsewhere (Frank, 1986a). Breeding occurs year-round (Frank, 1986a). Females have two teats, and 92% of zoo births were of litters of 1 or 2 cubs (Frank, 1986b). Females give birth in a separate natal den and bring their cubs to a communal den shared by other females when they are a few weeks old (East et al., 1989; Kruuk, 1972). From then on the cubs remain at the den, spending much of their time in burrows too narrow for adults to enter (East et al., 1989; Holekamp and Smale, 1990; Kruuk, 1972). Cubs are weaned at 9–18 months (Holekamp and Smale, 1990; Kruuk, 1972).

METHODS

Between 1978 and 1986 we observed the behavior of 39 female lions and their 78 cubs in the Serengeti National Park (2°30' S, 34°50' E) and the Ngorongoro Crater (3°15' S, 35°30' E), Tanzania, for a total of 656 h. Four females raised their cubs alone and the rest were grouped in 13 crèches. Two mothers were observed both before and after they joined crèches. The number of lactating females per crèche ranged from 2 to 4 (median, 2.3; mean, 2.7), litter size ranged from 1 to 4 (median, 2; mean, 1.9), and the number of cubs in each crèche ranged from 2 to 12 (median, 4.3; mean, 5.5). Only two of 39 litters were younger than 6 weeks old when first included in the study. The maximum age difference between cubs of lactating females in the

same crèche ranged 0–150 days (median, 40 days; mean, 51 days).

The composition of most crèches remained unchanged during the period of observation, but the litters of two females in one crèche were reduced by mortality, two crèches were joined by an additional female and cubs, and two females stopped lactating. Two crèches were accompanied continuously by cubs whose mothers had stopped lactating before the start of the observation period. These cubs are included in most analyses as “other cubs,” but are excluded in analyses of reciprocity between mothers.

The study areas and populations have been described in detail elsewhere (Packer et al., 1988; Schaller, 1972). The Serengeti population is large and outbred, while the Crater population is small and isolated (Packer et al., 1991b). The food supply is more seasonal in the Serengeti than in the Crater (Hanby et al., in press), and lions of the Serengeti have smaller body size (Packer C and Pusey AE, unpublished data) and suffer higher cub mortality (Packer et al., 1988).

We located lions by driving through the pride range, except for one crèche which could be located by radio telemetry. Observations were made for periods of 2–2.5 h at dawn and/or dusk, for a median total of 32.4 h per group (range, 7–89 h) over a median span of 55.4 days (range, 3–134 days). These time spans varied because of difficulties in finding the lions, variation in the length of our field seasons each year, and mortality of cubs.

All lions were well habituated to the presence of a vehicle and we observed them from a distance of 5–15 m with 8 × 35 binoculars. Individuals were identified by natural markings, particularly whisker spot patterns which are distinct even in small cubs (Packer and Pusey, 1993; Pennycuik and Rudnai, 1970). Maternity could be unequivocally determined in most litters either because the cubs were identified before their mother had mixed them with other cubs, or because size differences between cubs correlated with differences in the timing of the onset of lactation between females. We attributed maternity of all other cubs on the basis of maternal behavior (see below).

During each observation period we recorded the behavior of all females and cubs on standardized checksheets. All individuals could be observed simultaneously because females were relatively immobile, and cubs moved fairly slowly. One author usually acted as observer and the other as recorder. We noted the behavior of each cub as it approached each female to suckle, the position of the female, her response, the number of other cubs already suckling, the time of onset and termination of suckling and suckling attempts, the manner in which the suckling was terminated (by the female, cub, or another cub), and the time of onset and termination of all licking between cubs and females. A cub was recorded as suckling when it had a teat in its mouth. A female was recorded as nursing when a cub suckled from her. A suckling attempt occurred whenever the cub initiated suckling successfully or pushed its face close to the teat for longer than 2 s, but was kept off the teat by the mother or other cubs.

We determined independence between bouts of suckling attempts by plotting survivor curves of the intervals between the suckling attempts of each cub on each female (Slater, 1974). We found that suck-

ling attempts separated by less than 10 min belonged to the same bout, but attempts separated by longer intervals constituted separate bouts.

We collected milk from 15 female lions by tranquilizing each female, injecting her with 1 cc of oxytocin, and milking her by hand until no more milk could be extracted.

To compare the nursing behavior of lions and hyenas, we observed nine female hyenas and their 15 cubs at a communal den in the Ngorongoro Crater for a total of 42 h in January and February 1980, using the same methods. Litter sizes ranged from 1 to 2 (median, 2; mean, 1.67). The females were well habituated to vehicles and were easily distinguished by natural ear-notches, facial scars, and body color and markings. Hyena cubs could be reliably distinguished by size and color. Maternity of cubs was attributed on the basis of nursing behavior (see below).

Measures of nursing and suckling behavior

We computed the following measures to determine rates of nursing by females, and the way in which nursing was apportioned between their offspring and other cubs, both in the aggregate, and to each cub. *Total nursing*, the amount of suckling by each cub on the female divided by the total time she was observed. Thus, if a female nursed one cub for 7 min and another for 5 min over a period of 60 min total nursing would be $(7 + 5)/60 = 0.20$. *Nurse offspring*, the total suckling time by a female's own cubs divided by the total time she was observed. *Nurse other cubs*, the total suckling time by cubs belonging to other females divided by the total time the female was observed. *Nurse each offspring*, nurse offspring divided by number of offspring. *Nurse each other cub*, nurse other cubs divided by number of other cubs in the crèche. *Proportion of total nursing that went to cubs of other females*, nurse other cubs divided by total nursing. *Proportion of per capita nursing that went to each other cub*, nurse each other cub divided by the sum of nurse each other cub and nurse each offspring.

We measured the rate of suckling attempts that females received from offspring and other cubs as follows: *Attempts by offspring*, the total number of independent attempts (attempts separated by 10 min) by offspring divided by time observed. *Attempts by other cubs*, the total number of independent attempts by other cubs divided by time observed. *Per capita attempts by offspring*, attempts by offspring divided by number of offspring. *Per capita attempts by other cubs*, attempts by other cubs divided by number of other cubs.

The extent to which females opposed the suckling of their offspring and other cubs was determined by measuring their resistance to suckling attempts, and their termination of suckling bouts. *Resist offspring*, the proportion of independent suckling attempts of offspring resisted by the female (by snarling, biting, pushing, kicking, or rolling over). *Resist other cubs*, the proportion of independent suckling attempts from other cubs that were resisted by the female. *Difference in resistance rates of offspring and other cubs*, resist offspring minus resist other cubs. *Terminate offspring*, the proportion of independent suckling bouts (separated by 10 min) by offspring that were terminated by the

Table 1
Sign and *p* values of simple regressions between measures of nursing behavior and independent variables

	Across 35 females				Across 13 crèches			
	Own litter size	Other females' litter size	Cub age	Cub age difference	Kinship	Female belly size	Habitat	Kill
Total nursing	.34	.23	-.07	-.07	-.61	.07	.26	-.38
Nurse offspring	.05	.65	-.01	-.01	-.40	.13	.88	-.76
Nurse each offspring	-.42	.97	-.002	-.04	.95	.03	.66	-.27
Nurse other cubs	-.03	.63	-.97	.77	.66	.09	.04	-.14
Nurse each other cub	-.001	-.03	-.45	.41	.03	.01	.18	-.03
Proportion to others	-.0002	-.79	.05	.02	.13	.42	.04	-.12
Per capita proportion to others	-.005	-.007	.06	.002	.003	.39	.17	-.10
Attempts by offspring	.0001	.61	-.05	-.04	-.97	.18	.44	.43
Attempts by each offspring	-.23	-.34	-.005	-.26	.25	.03	.35	-.36
Attempts by other cubs	-.24	.37	-.84	.86	.88	.06	.02	-.43
Attempts by each other cub	-.01	-.02	-.30	.34	.03	.003	.003	-.12
Resist offspring's attempts	.69	-.27	.70	.18	-.85	.003	.04	-.80
Resist other cubs' attempts*	.46	-.85	-.30	-.94	-.20	.008	.10	.47
Resist own minus others*	-.43	-.75	.13	.23	.10	-.34	-.69	-.16
Terminate offspring's suckling	.17	.93	-.99	.36	.80	.07	.04	.60
Terminate other cubs' suckling*	-.71	-.55	-.06	-.80	.98	.03	.14	-.99
Terminate own minus others*	.08	.30	.26	.65	.78	.89	.37	.53

* *N* = 34 females for the across female analysis.

female. *Terminate other cubs*, the proportion of independent suckling bouts of other cubs that were terminated by the female. *Difference in termination rates of offspring and other cubs*, terminate offspring minus terminate other cubs.

We also examined suckling behavior from the point of view of cubs. *Total suckling*, total suckling time by the cub divided by total time observed. *Suckling from mother*, suckling time on mother divided by time observed. *Suckling from others*, total suckling time on other females divided by time observed. *Proportion of suckling from other females*, suckling from others divided by total suckling.

Independent variables

Kinship between females was scored as the probability that the females were first degree relatives (mother and daughter, or sisters). This measure was necessary because several females had been raised in crèches in which maternity was not precisely known but their mother could be narrowed to one of two or three females. *Own litter size*, the number of cubs in the female's own litter. *Other female's litter size*, the number of other cubs divided by number of other lactating females. This is equivalent to the mean litter size of the other mothers except in the crèches containing cubs whose mothers had stopped lactating. The results in this article are not altered if these cubs are excluded from the analysis. *Cub age*, the age of a female's litter. *Cub age difference*, cub age minus the mean age of other cubs in the crèche. *Belly size* varies greatly depending on recent food intake (Bertram, 1975) and was measured on a scale of 1 (fattest) to 5 (thinnest). *Habitat*, Ngorongoro Crater or Serengeti. *Kill*, the proportion of observation periods in which a prey carcass was present. *Group*, each female was categorized according to the identity of her group.

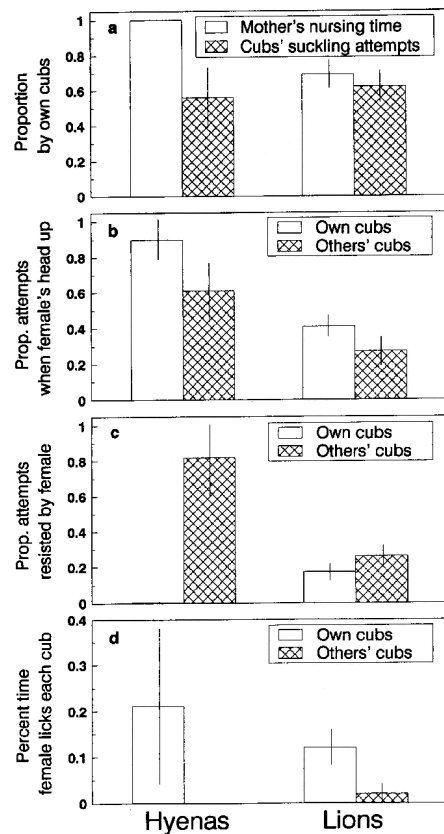
Analysis

Data were separated for each female according to whether her cubs were present during the observation, and whether she was lactating. Most of the analyses reported here were performed on the subset of females in crèches that were lactating and whose cubs were present during the observation period. Data were tallied within observations for each female and cub and then combined into time blocks totalling at least 7 h (median, 13 h; range, 7–27.6 h), covering spans of not more than 2 weeks when possible (median, 7 days; range, 2–42 days). Most of the analyses were first performed on the block data and showed the same general results as reported here. To avoid statistical dependence due to repeated measures, a weighted mean was then calculated for each dependent and independent measure for each animal observed for more than one time block. Similarly, individual cub means were combined to calculate a litter mean. To examine the effects of variables that were similar or identical for all group members (e.g., number of females in the group, kinship between females, female belly size, habitat, and kill), individual female or litter means were combined to calculate group means for mothers of the same crèche and litters of the same crèche.

Statistical tests were performed using Statistix (Analytical Software, 1992) or SPSS (SPSS, 1986). Where parametric statistics were used, the residuals were tested for normality with the Wilk-Shapiro statistic, and dependent variables were transformed appropriately where necessary. All probabilities are two-tailed. To test the effect of the independent variables on the nursing behavior of lions, we first used simple regressions to examine the effect of the relevant variable, and then used multiple regressions to control for potentially confounding variables. To provide a complete description of

Figure 1

Comparisons of the behavior of female hyenas and lions and their cubs. Vertical lines indicate standard errors. (a) Proportion of mothers' total nursing that went to their offspring ($n_1 = 9$ hyenas, $n_2 = 25$ lions, $z = -4.392$, $p < .0001$) and proportion of total suckling attempts received by females that were from their offspring ($z = -0.49$, ns). (b) Proportion of suckling attempts received by females from offspring and other cubs in which the female's head was up during the attempt (species difference with offspring, $n_1 = 9$ hyenas, $n_2 = 22$ lions, $U = 6$, $p = .0001$; species difference with other cubs $n_1 = 8$ hyenas, $n_2 = 21$ lions, $U = 8.4$, $p = .01$; difference between offspring and other cubs: hyenas, $T = 4$, $N = 7$ females, ns; lions, $T = 39$, $N = 21$ females, $p = .008$, Wilcoxon matched-pairs test). (c) Proportion of suckling attempts from offspring and other cubs resisted by females (species difference in resistance of offspring, $n_1 = 9$ hyenas, $n_2 = 24$ lions, $U = 25$, $p = .0009$, other cubs, $n_1 = 8$ hyenas, $n_2 = 23$ lions, $U = 4.5$, $p = .0001$; difference between offspring and other cubs: hyenas, $T = 0$, $N = 8$ females, $p = .01$; lions, $T = 62$, $n = 22$ females, $p = .04$). (d) Percent of time females licked their offspring and the cubs of other females (species difference in licking offspring, $n_1 = 9$ hyenas, $n_2 = 21$ lions, $U = 87$, ns, others' cubs, $U = 18$, $p = .0006$; difference between licking offspring and other cubs: hyenas, $T = 0$, $N = 7$ females, $p = .02$; lions, $T = 10$, $N = 20$ females, $p = .0004$).



nursing behavior, we present results of simple regressions of all the independent variables and all the dependent variables in Table 1. We provide the p value associated with each test even though a proportion of these may have arisen by chance because of the large number of tests. Because many of the dependent variables are similar to each other and some of the independent variables are correlated, the results of each test are not statistically independent. Therefore, a Bonferroni test that weighted all tests equally would likely be too conservative.

RESULTS

Species differences

Maternal visits to cubs

The two species differed in the synchrony of visits by females to their cubs. In lions, females of the same crèche stayed together and were generally either all present with their cubs or all absent. In contrast, female hyenas often arrived at or left the den singly, and on many occasions only one or two lactating females were present in the den. When female lions were not present, their cubs usually hid in thick vegetation or among rocks. Hyena cubs, in contrast, always hid in the burrows of the den. Female lions that had returned to their cubs by dawn usually stayed with them all day, while female hyenas generally rested away from the den during the day.

Nursing behavior

Lions often nursed other cubs but hyenas never did so (Figure 1a). Each female hyena was observed to nurse only the same one or two cubs throughout the study period, and these cubs were thus assumed to be the offspring of that female. In contrast, the 25 female lions whose cubs had been unequivocally identified gave about 30% of their total nursing to other cubs. This difference occurred despite the fact that females of each species received the same proportion of suckling attempts from cubs other than their own (Figure 1a).

The difference in non-offspring nursing between the two species appeared to result from differences in the behavior of the females. Female hyenas were more likely than female lions to be alert with their heads up during suckling attempts (Figure 1b), and female hyenas resisted a higher proportion of the attempts of other cubs by snarling, biting, pushing, and kicking (Figure 1c). In both species, females were less likely to be alert when other cubs attempted to suckle (Figure 1b).

Licking behavior

Female hyenas licked only their own offspring, while female lions licked other cubs as well as their own, although at significantly lower rates (Figure 1d). Female lions were licked by their offspring more than by other cubs (mean percent time licked by each offspring, 0.05%; SE, 0.03%; mean percent time licked by each other cub, 0.01%; SE, 0.004%; $N = 22$, $z = -3.3$, $p = .001$). Hyena females were licked at very low rates by any cubs, with no difference in the frequency that they were licked by offspring and other cubs.

Do female lions in crèches nurse more than singletons?

There was no evidence that lions in crèches nursed more than singletons. In multiple regressions controlling for litter size and cub age (singletons had significantly younger cubs and larger litters than females in crèches), there was no significant difference in the total nursing of singletons and females in crèches, nor did the total number of females have any effect on the total nursing of females ($N = 17$ groups).

Is nursing in lions indiscriminate?

Three lines of evidence show that female lions could discriminate between their own and other cubs. First, at the beginning of crèche formation, some females initially left their cubs hidden in a separate den and temporarily joined the other mothers and cubs. These females discriminated most strongly between their own and other cubs when their offspring were absent, never nursing other cubs during this time (Figure 2). Second, after females had mixed their cubs in a crèche, they still nursed each of their own offspring significantly more than they nursed each other cub (mean proportion of time females nursed each offspring = 0.084, SE = 0.033; each other cub = 0.025, SE = 0.01, $T = 8$, $N = 25$, $p < .0001$). Females also resisted a significantly higher proportion of suckling attempts by other cubs (Figure 1c) and terminated a higher proportion of the suckling bouts of other cubs, although

the latter difference was not significant (mean proportion of offspring's bouts = 0.38, SE = 0.08, of other cubs' bouts = 0.46, SE = 0.08, $N = 24$ females, $T = 113$, ns). Third, females nursed their offspring more exclusively after an absence from their cubs. On 17 occasions, some or all the females in a crèche were observed to return to their cubs after an absence of several hours and their mammae were obviously swollen with milk. For each female, we calculated the proportion of total nursing that went to her offspring in the first 10 min of nursing following her return and compared this to the remainder of that time block. Means were taken across all females that returned together and then across all returns within each crèche because females nursed synchronously following such returns and the data were statistically dependent. Females in each crèche nursed their offspring more exclusively following a return than at other times (proportion of total nursing that was of offspring: following a return = 0.83, SE = 0.29, during the rest of the time block = 0.65, SE = 0.27, $T = 6$, $N = 9$ crèches, $p < .05$).

Lion cubs also behaved differently towards their own mothers and other females. They made more suckling attempts on their own mothers (Figure 3a), they were less likely to wait until other cubs were already suckling from their mother before attempting to suckle (Figures 3b, 4), and they were more likely to announce themselves to their mother before attempting to suckle (Figure 3c).

The above data on lions (except nursing after a return) are based on females and cubs with known maternity. All other analyses include an additional 10 females whose cubs were already mixed in crèches when they were first observed. Maternity of each of these cubs is attributed to the female who nursed and licked them most often because these are such reliable measures of maternity.

Effect of kinship in lions

In crèches where kinship was highest, females nursed each other cub more and gave a higher per capita proportion of nursing to other cubs (Table 1; Figure 5). The latter effect remains significant in a multiple regression controlling for litter size and cub age ($t = 4.87$, $p = .0009$; R^2 for whole model = .88, $p = .0002$, $N = 13$ groups). The per capita proportion of nursing to other cubs would be 0 if females nursed their offspring exclusively, 1.0 if mothers exclusively nursed other cubs, and 0.5 if nursing was apportioned equally across all cubs. Figure 5 shows that mothers were virtually indiscriminate when all females in the group were first order relatives. The per capita rate of suckling attempts by other cubs also increased with kinship, and females were less likely to resist other cubs compared to their own as kinship increased, but this latter trend was not significant (Table 1).

Five of the 13 crèches contained females with a range of kinship classifications (e.g., two sisters and a cousin). In all five cases, females nursed each cub of their closest kin more than those of their more distant kin ($p = .06$, two-tailed, sign test).

Effect of litter size in lions

The total nursing by females in crèches was not significantly correlated with their own litter size

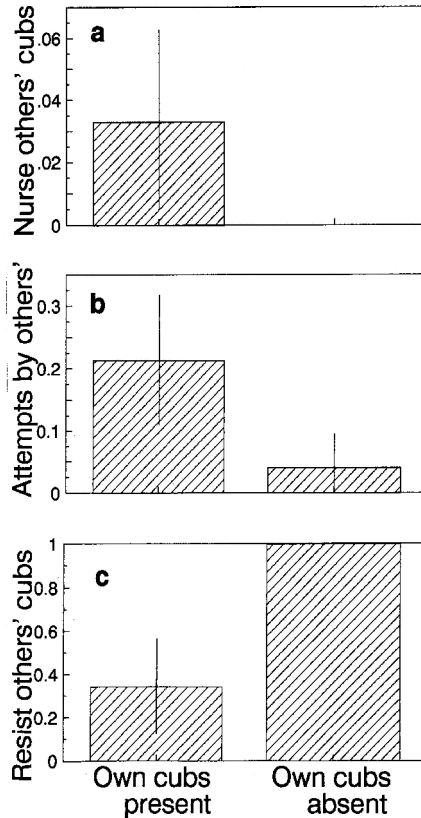


Figure 2

(a) Proportion of time female lions nursed each cub of other females when their offspring were present or absent ($T = 0$, $N = 6$ females, $p < .05$). (b) Number of independent nursing attempts received per hour by female lions from each other cub when their offspring were present or absent ($T = 0$, $N = 6$ females, $p < .05$). (c) Proportion of nursing attempts from other cubs that females resisted when their offspring were present or absent ($T = 0$, $N = 2$ females, ns).

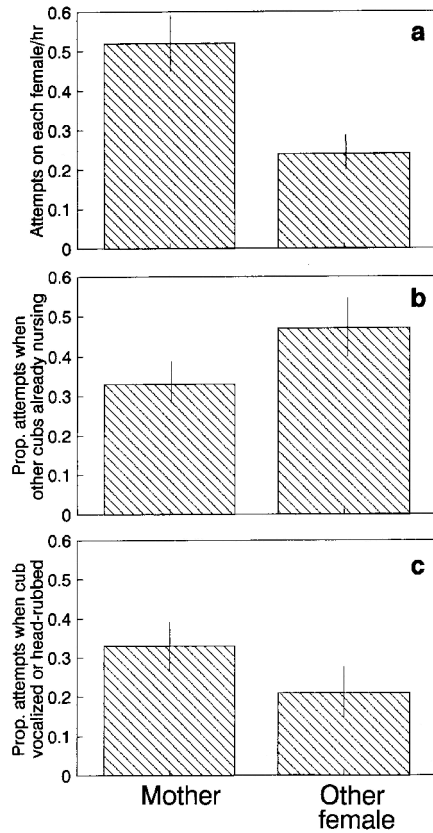
(Table 1; Figure 6a), but the proportion of nursing that they gave to other females' cubs decreased significantly with increasing litter size (Table 1; Figure 6b). This is a robust effect that remains significant after controlling for other factors that strongly affected this measure (age, habitat, and group, $t = -3.64$, $p = .002$). Although per capita attempts by other cubs decreased significantly as female litter size increased, litter size had no significant effects on the rates at which females resisted the suckling attempts or terminated the suckling bouts of their own or other cubs (Table 1).

Cubs appeared to be sensitive to differences in the litter sizes of other females. Twelve litters of cubs could choose within their crèche between females with litters of different sizes. In nine cases cubs suckled more from the female with the smaller litter (Wilcoxon matched pairs test, $T = 10.5$, $p = .028$, $N = 12$).

The litter size of other females had no significant effect on the nursing rate or proportion of total nursing to other cubs either in simple regressions (Table 1), or multiple regressions controlling for female's own litter size and other factors that strongly affected these measures. The lack of a significant effect of this factor may be due to the fact that "other females' litter size" is an average across other females in the same crèche and therefore dampens the effects of large differences in litter size. Females received fewer attempts from each other cub, gave less nursing to each other cub, and

Figure 3

(a) Number of independent suckling attempts per hour by lion cubs on their mother and on each other female ($z = -5.8$, $N = 53$ cubs of known maternity, $p < .00001$). (b) Proportion of independent suckling attempts by lion cubs on their mother or on other females in which other cubs were already suckling from the female ($z = -3.1$, $N = 45$ cubs, $p < .01$). (c) Proportion of independent suckling attempts by cubs on their mother or on other females in which the cub vocalized or head-rubbed the female immediately before the attempt ($z = -3.4$, $N = 45$ cubs, $p < .001$).



gave a lower proportion of per capita nursing to other cubs as their companions' litter size increased (Table 1). These results presumably reflect the fact that the total nursing a female gives to other cubs is divided among a larger number of cubs as the litter size of other females increases.

Effect of lion cub age

Although suckling rates follow an inverse U-shaped curve with age in many species, lion cubs cannot be observed until they reach peak suckling rates. In this study the logarithm of total suckling by cubs decreased linearly with age ($t = -3.26$, $p = .003$, $N = 35$ litters). As the age of their offspring increased, females nursed offspring significantly less, and they gave a higher proportion of total and per capita nursing to other cubs (Table 1). The effects of age on the proportional measures of nursing remained significant in multiple regressions controlling for other significant factors (proportion of total nursing to others, controlling for own litter size, habitat and group, $t = 2.52$, $p = .02$; per capita proportion to others, controlling for kinship, own litter size, other females' litter size, group, $t = 2.17$, $p = .04$). Although females tended to resist the attempts of other cubs more when their offspring were young, there were no significant changes with age in female resistance or termination of suckling (Table 1).

The presence of older cubs did not interfere with a female's nursing of her own offspring. Of 43 supplants of one cub by another that terminated a suckling bout for at least 10 min, 37 involved a younger cub being supplanted by an older one. However, across cubs, a mean of only 2.8% of suckling bouts were terminated by the supplanting behavior of another cub (median = 0, range = 0–50%, $N = 70$ cubs). The only two cubs that were supplanted at high rates were both less than two months old. When these cubs were excluded, the rate of successful supplants was even lower (mean = 1.4%, median = 0, range = 0–11%, $N = 68$ cubs). If older cubs generally prevented young cubs from suckling, we would expect females to lose a higher proportion of nursing to other cubs when their own offspring were relatively young. Instead, the age difference between a female's offspring and the other cubs had a significantly positive effect on both the proportion and per capita proportion of nursing that went to other cubs (Table 1). Females nursed

Figure 4

Lion cub surreptitiously approaches to suckle from a female that is not its mother. The female is already nursing two of her own cubs and one larger cub of another female. Photo by Craig Packer.



other cubs proportionately little when their offspring were younger than others, and nursed others proportionately more when their own offspring were older than the rest. Age difference is significantly correlated with cub age ($R = .51, N = 35, p = .002$), but after offspring's age was controlled in a multiple regression, females still gave a higher per capita (but not total) proportion of nursing to other cubs when their offspring were older than the others ($t = 2.59, p = .01, N = 35$). Age difference had no significant effects on measures of female resistance either in simple regressions (Table 1) or multiple regressions controlling for offspring's age.

Effect of milk and meat availability in lions

Female belly size

Our data from milk extraction suggest a correlation between milk availability and female belly size. We were able to extract more milk from fat than thin females (Figure 7). Because the mean belly size of mothers is positively correlated with the mean belly size of their litters ($R = .48, p = .006, N = 32$ litters), the cubs of thin females are likely to be in greater need of milk. Thin females, therefore, might be expected to restrict their milk more exclusively to their own offspring. On the other hand, because belly size among females in the same group is more similar than among females of different groups (ANOVA $F_{1,18} = 3.67, p = .007$), the cubs of the other females are likely to be just as hungry as the female's offspring and thus more likely to steal milk. However, female belly size had no significant effect on the exclusivity with which females nursed their own offspring. Females in thin groups received significantly more suckling attempts from each offspring and each other cub, and they nursed each significantly more, despite the fact that females showed higher rates of resistance and terminations when they were thin (Table 1). Because thin females nursed each cub more, there was no significant effect of female belly size on the proportion of total nursing that went to other cubs, or the per capita proportion that went to other cubs (Table 1).

Although the belly sizes of females in the same crèche were highly correlated, differences were observed in several cases. We tested whether cubs of females that were thinner than their companions might compensate for the lack of milk from their mothers by nursing more from other females. There were 21 females who were sometimes thinner and sometimes fatter than their companions. For each of their cubs the mean suckling time on each other female was calculated separately across observations when its mother was thinner or fatter than that female. There was no significant difference in cub suckling time on others between each condition (21 cubs suckled more from others when their mothers were thinner than their companions and 20 cubs suckled less). Some females were consistently thinner or fatter than their companions over all observation periods. To determine whether litters of thinner females were able to gain as much access to milk as the other cubs we tested the effect of the difference between mother's belly size and the average belly size of her companions on cub suckling measures in a cross-litter analysis. We controlled for mother's belly size because mother's

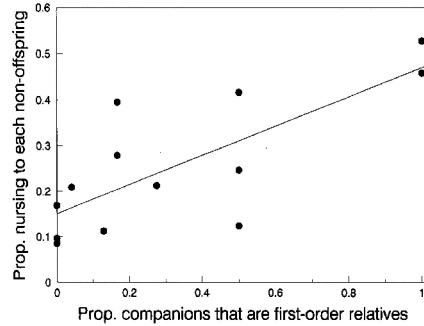


Figure 5
The mean per capita proportion of nursing by all females in each crèche that went to other cubs (see text) plotted against the probability that all females in the crèche are first-order relatives ($R^2 = .58, p = .003, N = 13$ crèches).

belly size is significantly correlated with belly size difference ($R = .50, p = .0034, N = 33$ litters), and cubs suckle at higher rates when their mothers are thin (Table 1). We found that litters suckled significantly less in total, and significantly less from their mothers, when their mothers were thinner than their companions (belly size difference versus total suckling: $t = -3.175, p = .0035, N = 33$; belly size difference versus suckling on mother: $t = -3.98, p = .0004, N = 33$), but did not compensate by suckling significantly more from other females or gaining a higher proportion of their suckling from other females.

Habitat and kill

There is some evidence that females in harsher habitats may have more limited supplies of milk (Oftedal OT, Packer C, and Pusey AE, in preparation), and habitat affected several measures of nursing behavior (Table 1). Serengeti females gave more nursing time to other cubs and proportionately more of their total nursing to other cubs than those in Ngorongoro Crater. They received more suckling attempts from other cubs, and were more likely to resist the attempts and terminate the suck-

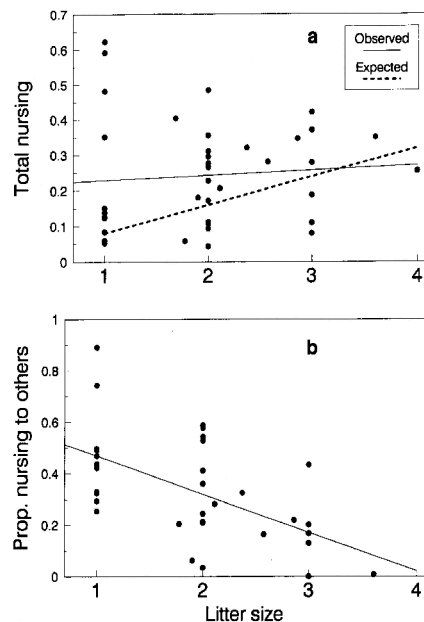
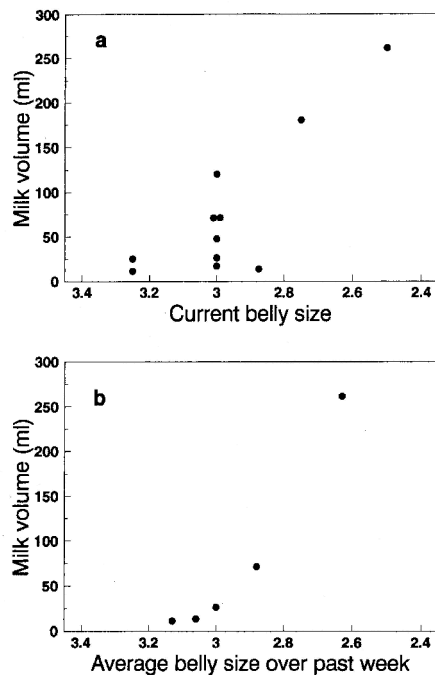


Figure 6
(a) Rate of total nursing (nurse all cubs) by females with different litter sizes. The narrow line shows the regression line of total nursing against own litter size ($R^2 = .03, N = 35$ females, ns). The dotted line shows the expected rate of nursing if females only nursed their offspring and nursed each at the rate reported in the text. (b) The proportion of a female's total nursing that goes to other cubs plotted against her own litter size ($R^2 = .34, p = .0002, N = 35$ females).

Figure 7
Volume of milk extracted by hand from females plotted against (a) her belly size on the day of extraction, and (b) her average belly size over preceding week. A high belly size score is thin and a low number is fat.



ling bouts of their offspring. There was a nonsignificant tendency for females to be thinner in the Serengeti ($R = .49$, $N = 13$ groups, $p = .09$). When we controlled for female belly size in multiple regressions, habitat no longer had any significant effects.

In the presence of a kill, cubs are able to eat meat. They may therefore be less motivated to suckle and make fewer attempts from other females. The presence of a kill had a significant negative effect on nursing of each other cub, and a nonsignificant negative effect on most other measures of nursing including the proportion and per capita proportion of nursing to other cubs (Table 1). Females tended to be fatter when a kill was present

Table 2
Differences between groups in generosity

Measure of generosity	<i>F</i> scores and significance of regressions testing the	
	Effect of group (df 11,19)	Effect of group after controlling for other factors (df 10,15)
Nurse other cubs	1.57	1.60
Nurse each other cub	3.81**	1.54
Proportion of total nursing to other cubs	0.91	0.61
Per capita proportion of nursing to other cubs	3.66**	0.72

** $p < .01$.

Table 3
Extent to which pairs of females within six groups reciprocated in nursing each other's cubs

Group size	<i>F</i> when $p = .5$	<i>F</i> values of ANOVAS of the ratio of between pair to within pair variance in	
		Raw data	Residuals
3	0.88	0.08 -	0.09 -
3	0.88	0.78 -	0.78 -
3	0.88	5.83 +	2.32 +
3	0.88	2.39 +	1.99 +
3	0.88	0.12 -	0.29 -
4	0.98	0.77 -	0.65 -

+ indicates reciprocity and - indicates asymmetry (see text).

($R = -.31$, $N = 13$ groups, $p = .30$), and the inclusion of female belly size in a multiple regression removes the significant effect of kill.

Testing for reciprocity in lions

We tested for evidence of reciprocity in both an across-group and a within-group analysis. If females show reciprocity in nursing each other's young, we would expect females in the same group to show similar levels of generosity, while levels of generosity between groups might vary from total selfishness to great generosity. There are several possible measures of generosity: the total amount of nursing a female gives to others, the total proportion of her nursing that she gives to others, the total amount she gives to each other cub, and the amount she gives to each other cub relative to the amount she gives each of her own (per capita proportion). Rather than make any assumption about how females might assess each other's generosity, we have tested all these measures. Two measures of generosity showed significant variation between groups (Table 2). However, in multiple regressions that controlled for factors that strongly affected nursing at the level of the group (litter size, kinship, female belly size, habitat, kill), groups no longer differed significantly in any measure of generosity (Table 2). Thus, the effect of group membership on measures of nursing appears to be due to independent factors that affect all females in the group rather than to any group-level "negotiations" of nursing rates.

In groups of three or more females, each female could conceivably "choose" to nurse the cubs of her companions according to each companion's generosity toward her own offspring. To test this possibility, we examined both the scores for each measure of generosity and the residuals of each measure for each female obtained by controlling for group, kinship, litter size, other female's litter size, and cub age. We then performed ANOVAs on the raw scores and the residuals for all pairs of females within the group to calculate the ratio of between-pair to within-pair variance for each group. It is not appropriate to calculate the significance of *F* values for individual groups because there is dependence between female scores in the same group. For example, reciprocal nursing between one pair of females in the same group is likely to

affect the levels of nursing between other pairs in that group. Instead, we determined whether the F values for the respective groups were all high, indicating widespread reciprocity, or low, indicating that relationships are generally asymmetrical. To classify F values as high or low, we took the F value for each group size for which $p = .5$ and scored the number of groups with F values above and below that value. Table 3 shows F values for six groups for one measure of generosity, nursing each other cub. Four of the six groups had low F values, indicating asymmetry rather than reciprocity, although the overall trend across groups is not significant. Similar patterns were found with the other three measures of generosity, and in no case did all groups show high F values.

Effect of lion cubs' sex

In several species, mothers nurse sons more than daughters (e.g., Clutton-Brock et al., 1981; Lee and Moss, 1986). However, female lions do not nurse sons more. Across cubs, sex had no significant effect on any measure of suckling, suckling attempts, or mother's resistance. In lions, the lifetime reproductive success of males depends more on the number of like-sexed individuals in their cohort than does the reproductive success of females (Packer and Pusey, 1987). We might therefore expect females to invest more in male non-offspring, particularly if they have sons, thus ensuring that their sons or male relatives have male companions with which to cooperate. Across females, neither the sex ratio of the female's own litter, sex ratio of other cubs, nor total sex ratio of cubs in the crèche had any significant effect on any measure of nursing, suckling attempts, resistance, or terminations. Because only those females whose own litter contained males would benefit directly from male-male cooperation, we repeated the analysis for only those females that had at least one son in her litter. The sex ratio of other cubs in the crèche had no effect on any aspect of the nursing behavior of mothers with sons.

DISCUSSION

Is time spent nursing a good measure of milk transfer?

In this study, as in other field studies of nursing behavior (reviewed in Clutton-Brock, 1991), we use nursing time as the measure of milk transfer. This assumes that nursing time is positively correlated with milk transfer. However, we were able to extract less milk from thin females than from fat females, and cubs suckled longer from thin females. Thus, as in some other species (Mendl and Paul, 1989), lion cubs may sometimes suckle more when less milk is available. This presumably reflects greater effort by cubs to procure limited quantities of milk. However, this does not affect any of our conclusions concerning the generosity of females towards non-offspring. Our two proportional measures compare nursing time of other cubs to nursing of offspring under the same conditions, and we controlled for milk availability whenever we used non-proportional measures to measure generosity.

Species differences in the extent of non-offspring nursing

Spotted hyenas only rarely show non-offspring nursing (Knight et al., 1992) and the hyenas observed here never nursed cubs other than their own. In contrast, female lions gave about a third of their nursing time to others. This difference may occur both because of species differences in the costs of vigilance against milk theft by non-offspring and because of differences in the costs of lost milk. Hyena females received the same proportion of suckling attempts from non-offspring as female lions, but they were more alert and resisted a higher proportion of the attempts of other cubs. They may be able to afford these higher levels of vigilance because they spend comparatively little time with their cubs, presumably because their cubs hide in secure burrows. Indeed, female hyenas never resisted the nursing attempts of their own offspring (Figure 1c), suggesting that the main purpose of their visit to the den was to nurse their young. Lions, in contrast, leave their cubs only for brief periods when they go off to hunt. While they are resting with their cubs, female lions are faced with frequent suckling attempts and may incur greater costs from remaining alert and discriminating between cubs. It is noteworthy that female lions were more likely to nurse their offspring when they first came back to them and were still awake.

There are three reasons why hyenas may suffer higher costs from milk loss. First, they have smaller litter sizes than lions. Hyenas, with only two teats, are adapted to producing milk for a maximum of two cubs, and intensive competition between hyena cubs sometimes leads to siblicide, suggesting that female hyenas may sometimes be able to provide for only one cub (Frank, 1986b; Frank et al., 1991; Hofer H and East M, in preparation). Second, hyena cubs are weaned later than lion cubs (9–18 months versus 6–8 months) and are more exclusively dependent on milk than lion cubs. While most lion cubs eat meat regularly by the age of 3 months, hyena cubs do not usually have access to meat until they are at least 6 months old (Frank, 1986b; Holekamp and Smale, 1990; Kruuk, 1972). Therefore, female hyenas may benefit more from nursing only their own offspring. Third, because mean group size is generally greater in hyenas than in lions, mean kinship between females will be lower. It is significant that the only cases of non-offspring nursing observed in hyenas occurred between close relatives, and in at least one of these cases each female only had one cub (Knight et al., 1992; East M and Hofer H, personal communication).

Factors influencing non-offspring nursing in lions

In accordance with the predictions outlined in the introductory remarks, female lions nursed non-offspring most often when the costs were lowest. First, non-offspring nursing was most frequent between close kin. In crèches where females were first-order relatives, they nursed their own and other cubs equally, and, within each crèche, females gave the most nursing to the cubs of their closest relatives. Second, females with small litters nursed as much

as females with large litters, but gave more nursing to non-offspring. Mothers with small litters presumably have the most milk to spare to non-offspring. Third, female lions gave a higher proportion of their nursing to other cubs as their offspring increased in age. Because the oldest cubs in this study suckled the least and ate the most meat, they would therefore suffer least from diversion of their mother's milk.

Lion crèches possess the conditions of stability and small group size that are conducive to the evolution of reciprocity (Boyd and Richerson, 1988). However, we found no evidence of reciprocity either within whole groups, or between pairs of females within groups. There were large differences between individual females in the degree to which they nursed non-offspring, even after the effects of litter size, kinship, and cub age had been removed. Thus, nursing relationships often showed a one-sided, rather than a reciprocal, pattern.

Both females and cubs may be responsible for the adaptive variations in non-offspring nursing. In general, females resisted the attempts of other cubs more than they resisted their own offspring (Figure 1c), and this difference was even more extreme when their own cubs were young and when the other cubs were distant kin, although these trends did not reach significance (Table 1). By limiting the analysis of resistance and terminations to independent attempts, we could often include only one or two events per observation period and may therefore have missed finer-level differences in the rejectiveness of females. However, females may also have been limited in the extent to which they could reject other cubs by the cubs' surreptitious behavior (Figure 3c), or by the costs of disrupting the suckling of offspring [because non-offspring often waited until a female was already nursing her offspring before attempting to suckle (Figure 3b)].

Although cubs could theoretically improve their inclusive fitness by nursing parasitically from other females, thereby decreasing their mother's reproductive effort, they are at least partly constrained by the behavior of other females to suckle primarily from their mothers. Furthermore, cubs may benefit by suckling regularly from their mother, because a continuous milk supply depends on consistent rates of nursing (Mepham, 1976). If cubs monopolized their own mother when milk was most valuable to them, non-offspring would have few opportunities to suckle, further reinforcing the low levels of milk theft in these situations.

Why do female lions form crèches?

Our results do not support the view that communal nursing confers significant nutritional benefits on young. Females in crèches do not nurse any more than singletons, so cubs in crèches do not generally gain access to more milk. The cubs of a small proportion of females do appear to benefit from crèching, because females with smaller litters give a higher proportion of their nursing time to non-offspring, making it advantageous for females with large litters to join them in a crèche. However, in these cases mothers of small litters lose substantial quantities of milk to non-offspring, and when both fe-

males have large litters there will be no nursing advantage to either female. Our long-term demographic data show that Serengeti cubs suffer higher mortality as the size of the other litters in their pride increases from two to four cubs (Packer C and Pusey AE, unpublished data). No such effect is observed in the food-rich Ngorongoro Crater, but neither is there any indication of a nutritional advantage of crèching on cub survival in the Crater. Our previous work on hunting success showed that the typical number of adult females in crèches is often suboptimal for female foraging efficiency (Packer et al., 1990), and an analysis of belly size showed that mothers in crèches with three or four females suffered lower mean food intake than singletons or pairs (Packer, 1986).

Even if cubs in crèches do not gain access to more milk, it might be supposed that cubs could benefit from a reduction in the variance of meal frequency or meal size (see introductory remarks), but this is unlikely in lions. Female lions visit their cubs synchronously, and belly sizes of females in the same crèche are highly correlated. Therefore, cubs do not usually have an opportunity to nurse from a well-fed female when their mother is thin or absent. On those occasions when females did vary in belly size, the cubs of thin females did not increase their nursing from other females.

The most compelling advantage of forming crèches appears to be the communal defense of cubs against invading males. Infanticide by male lions accounts for 27% of cub mortality (Pusey and Packer, 1987). Mothers actively defend their cubs from potentially infanticidal males (Packer and Pusey, 1983a, 1984; Pusey and Packer, 1994) and females in groups are better able to defend their cubs (Packer et al., 1990). To defend their cubs, female lions need to remain with them as much as possible. Because they must therefore rest and sleep in close proximity to the entire brood of cubs, female lions are inevitably subject to milk theft from non-offspring. But the close kinship between female lions (Bertram, 1976; Packer et al., 1991a) may make the costs of losing some milk to non-offspring lower than the costs of remaining sufficiently vigilant to prevent all losses. A similar explanation has recently been proposed to account for communal nursing in populations of house mice (Manning et al., in press). Communally raised mice pups do not gain obvious nutritional advantages, but they are much less likely to die from infanticide, and females share nests with close relatives.

Because female lions are likely to benefit from the cooperative defense of their cubs as soon as they are born, we may ask why they wait to pool their cubs until they are at least 6–8 weeks old. Age differences between litters have been shown to reduce the survival of the younger litter in rats (Menella et al., 1990), and in this study the cubs of the two litters less than 2 months old were subjected to higher rates of supplants by other cubs. Cubs aged 2 months or older, however, did not suckle less in the presence of older cubs, suggesting that after they are 6–8 weeks of age cubs can maintain access to their mother's teats in the presence of older cubs. Thus, at least in terms of access to milk, there do not seem to be any costs from mixing cubs above this age.

Conclusions

The detailed comparison of nursing behavior in lions and hyenas supports our larger cross-species survey (Packer et al., 1992) in identifying litter size and kinship as important factors affecting the incidence of non-offspring nursing. Costs of vigilance against milk theft by non-offspring also appear to be important. The lion study suggests that kin selection plays a greater role than reciprocity or mutualism in explaining the distribution of non-offspring nursing among females. Finally, the fact that communal nursing in lions does not appear to confer strong nutritional benefits raises the question of whether most other species that show extensive non-offspring nursing do so because females are constrained, like lions, to keep their young together for other reasons.

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