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# NOTES AND COMMENTS

## THE LACK CLUTCH IN A COMMUNAL BREEDER: LION LITTER SIZE IS A MIXED EVOLUTIONARILY STABLE STRATEGY

Following David Lack's (1947) hypothesis for the evolution of clutch size, several models have been developed to explain why vertebrate clutch sizes are generally smaller than the size that maximizes short-term reproductive success (reviewed in Stearns 1992). First, animals may show "individual optimization," where parents with inadequate resources rear smaller broods than those with the highest resource base. Individual optimization has been confirmed in birds (Pettifor et al. 1988) and may also occur in rodents, where litter size varies with the mother's nutritional state (see, e.g., Dobson and Murie 1987; Festa-Bianchet and King 1991). Second, smaller broods may be favored by evolutionary "bet hedging" (Phillipi and Seger 1989). Small broods may be more viable than larger broods during periods of hardship and thus confer higher geometric mean fitness in variable environments (Boyce and Perrins 1987; but see Liou et al. 1993). Third, smaller brood sizes may be favored by the trade-off between the parents' current and future reproductive effort or between the quantity and quality of offspring in each brood (Gustafsson and Sutherland 1988; Daan et al. 1990; Stearns 1992).

Finally, several models have emphasized game-theoretic aspects of brood size in insects (Parker and Courtney 1984; Smith and Lessells 1985; Parker and Begon 1986), but vertebrate studies have neglected the possible effects of neighbors' clutch sizes on parental payoffs. Here we present evidence from African lions that the productivity of a female's litter depends on the sizes of her companions' litters. We view communal rearing in lions as a discrete-strategy game in which large litter sizes can invade populations with small litter sizes and vice versa. We suggest that the "optimal" litter size in lions is frequency-dependent (Maynard Smith 1982) and that the observed *distribution* of litter sizes is adaptive.

Over 20 lion prides in northern Tanzania have been studied continuously since the mid-1960s (Packer et al. 1991*a*, 1991*b*); each pride is censused several times per month, and all animals are recognized by natural markings (Packer and Pusey 1993). We have data on 469 litters of known size. Litters are not observed until the cubs are a few weeks old, but postpartum litter size in lions is virtually identical to litter size in utero (Smuts et al. 1978). We define "productivity" as the number of cubs to survive to 1 yr of age because infant mortality is highest

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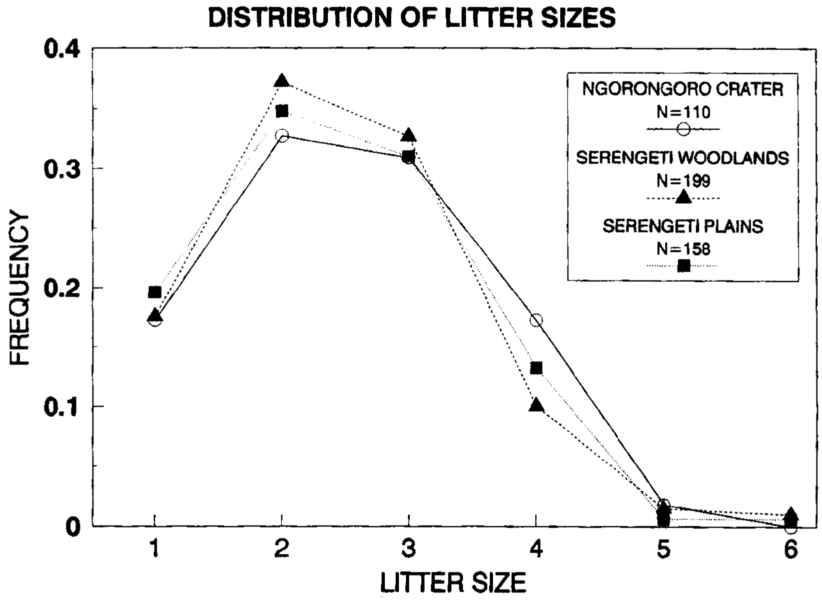

FIG. 1.—Distribution of litter sizes in three different habitats: Ngorongoro Crater (*open circles*), the Serengeti Woodlands (*solid triangles*), and the Serengeti Plains (*solid squares*). There is no significant variation in litter size across habitats ($\chi^2 = 5.659$, df = 10, $P = .8430$), in spite of striking differences in maternal nutrition.

in the first few months and mortality cannot be distinguished from dispersal at greater ages (Pusey and Packer 1987; Packer et al. 1988).

Over 98% of lion litters contain one to four cubs, with almost 70% containing two or three cubs (fig. 1). Females show no correlation between their own litter size and the litter size of their mothers (discrete [Poisson] regression, coefficient: SE = −0.02, $n = 84$ females of known maternity, $P = .9840$), nor do individual females show any consistency in the size of their litters (Kruskal-Wallis, $H = 60.60$, $n = 190$ litters, df = 53, $P = .2207$; based on 54 females that each had at least three litters of known size). Thus each female lion generates a distribution of litter sizes, with two to three being the most common.

Food consumption of the lions we studied is consistently highest in the Ngorongoro Crater (Hanby et al. 1995), whereas in the Serengeti, the annual migration of the ungulates results in a seasonal food supply (Schaller 1972). Within our Serengeti study area, food intake is lower in the plains than in the woodlands (Packer et al. 1988; Scheel and Packer 1995). Despite these differences in food supply, however, the distribution of litter sizes remains constant across habitats (fig. 1). Thus the variation in lion litter size cannot be explained by individual optimization.

Does maternal fitness vary with litter size? In the food-rich Ngorongoro Crater, the number of surviving offspring increases linearly with increasing litter size (fig. 2). In the Serengeti, productivity varies according to annual rainfall: during "good

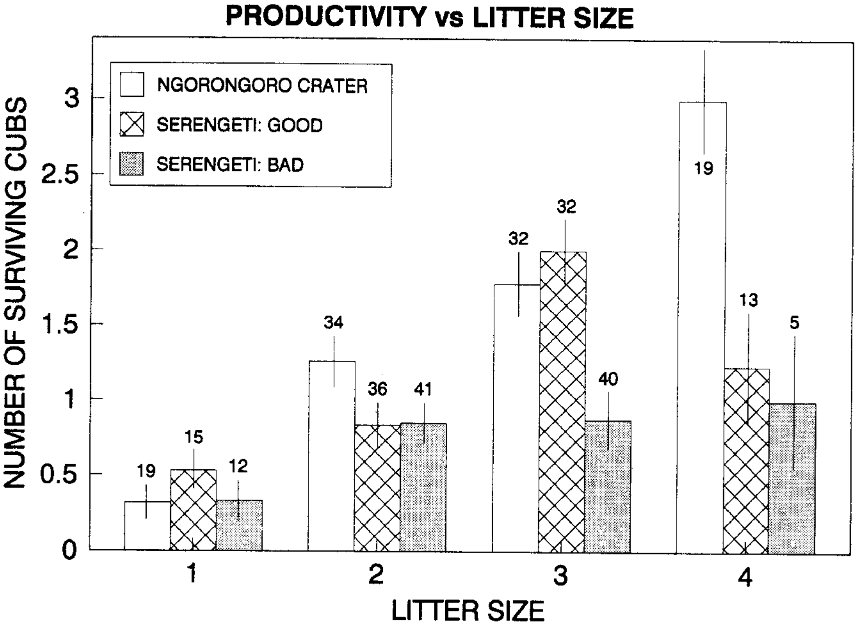

FIG. 2.—Average number of surviving offspring from litters of each size for each level of maternal nutrition: Ngorongoro Crater (*open bars*), good years in the Serengeti (*cross hatched*) and bad years in the Serengeti (*shaded*). Vertical lines indicate standard errors. The number of surviving offspring varies significantly with litter size both in the crater (Kruskal-Wallis, $H = 36.06$, df = 3, $P < .0001$) and during good years in the Serengeti ($H = 21.82$, $P = .0001$), but not in bad years in the Serengeti ($H = 2.79$, $P = .4249$). The number of surviving offspring increases significantly with increasing litter size in the crater (discrete [Poisson] regression, coefficient:SE = 6.58, $P < .0001$) and in good years in the Serengeti (coefficient:SE = 3.54, $P < .001$). Across habitats, there is no significant difference in productivity for litters of one or two cubs. For litters of three, litters born in bad years in the Serengeti show significantly lower productivity than litters born either in the crater (Mann-Whitney $U$-test, $P < .01$) or in good Serengeti years ($P < .001$). For litters of four, the crater shows significantly higher productivity than either good ($P < .01$) or bad ($P < .02$) years in the Serengeti.

years" dry-season rainfall is above average and wet-season rainfall is below average, the migratory herds are abundant in our study area for longer periods, and lion productivity reaches a peak at a litter size of three. During "bad years," dry-season rainfall is below average, wet-season rainfall is above average, the migratory herds spend less time in our study area, and lion productivity does not increase significantly with increasing litter size.

Lion productivity is clearly limited by food: four-cub litters survive best in the crater (where food is most abundant), three-cub litters survive well both in the crater and during good years in the Serengeti (when food is at least moderately abundant), and litters of one to two cubs can be reared as successfully in harsh conditions as under other circumstances (fig. 2). Although large litters are affected significantly more by food availability than are small litters, their productivity is never lower than the smaller litters'. Thus the geometric mean productivity is highest for litters of three in the Serengeti, whereas the optimum litter size appears to be four in the crater. Yet in each habitat litters of two and three cubs are by far the most common.

Can the high incidence of small litters be explained in terms of life-history trade-offs? Neither the initial litter size nor the number of surviving offspring from the current litter has any significant effect on (*a*) a female lion's subsequent litter size (initial litter size: coefficient:SE = $-0.71$, $n = 31$ females for whom consecutive litter sizes were known, $P = .4752$; number of surviving cubs from first litter: coefficient:SE = $-0.61$, $n = 31$, $P = .5401$), (*b*) the mother's survival over the following 4 yr (initial litter size: logistic regression, coefficient:SE = 0.71, $n = 436$ litters, $P = .4779$; number of surviving cubs: coefficient:SE = 1.00, $n = 390$ litters of females that survived at least 1 yr after giving birth, $P = .2921$), or (*c*) the lifetime reproductive success of daughters (initial size of litter into which daughter was born: discrete [Poisson] regression, coefficient:SE = $-0.98$, $n = 67$ daughters, $P = .3293$; number of surviving cubs in litter that daughter was born: coefficient:SE = $-0.20$, $n = 67$, $P = .8439$).

In sum, lion litter sizes do not conform to predictions of individual optimization and are smaller than expected on the basis of bet hedging or life-history trade-offs. However, none of these approaches measure the effects of a female's companions on her reproductive success. Female lions usually rear their young in groups: mothers typically pool their cubs in a crèche of two to three females, nursing and feeding each other's young until they reach 1.5 yr of age (Packer et al. 1990; Pusey and Packer 1994). Thus the litter size of their companions should also be considered in any analysis of an optimal litter size.

Variation in pride size enables us to test for the effects of group living on the productivity of each litter size. A small proportion of female lions live as solitaries (Packer et al. 1988, 1990), and although solitary females are as successful as group-living females in rearing small litters, they are less able to rear large litters in the Serengeti (fig. 3). Communal rearing attenuates the density-dependent effects of rearing large litters because the mothers of each crèche give birth to a distribution of litter sizes, and mothers of large litters gain additional care for their cubs from the other mothers. Females with small litters nurse as often as females with large litters, and they nurse nonoffspring more frequently than do mothers of large litters (Pusey and Packer 1994).

Although group rearing may reduce density-dependent mortality at the level of individual mothers, density dependence will still be expected to operate at the level of the crèche (Parker and Begon 1986). When Serengeti females give birth within 90 d of their pridemates, their own litters' productivity varies significantly with the litter size of their companions (fig. 4*A*). The lower productivity of females paired with mothers of a single cub probably results from the fact that mothers of single cubs often abandon the cub (Packer and Pusey 1984) and do not join a crèche. When the analysis is restricted to companions with litters of two or more cubs, the productivity of a Serengeti female declines significantly as her companions' litter size increases (fig. 4*A*).

Table 1 presents payoff matrices for mothers of each pride that gave birth within 90 d of each other, showing the productivity of each litter size according

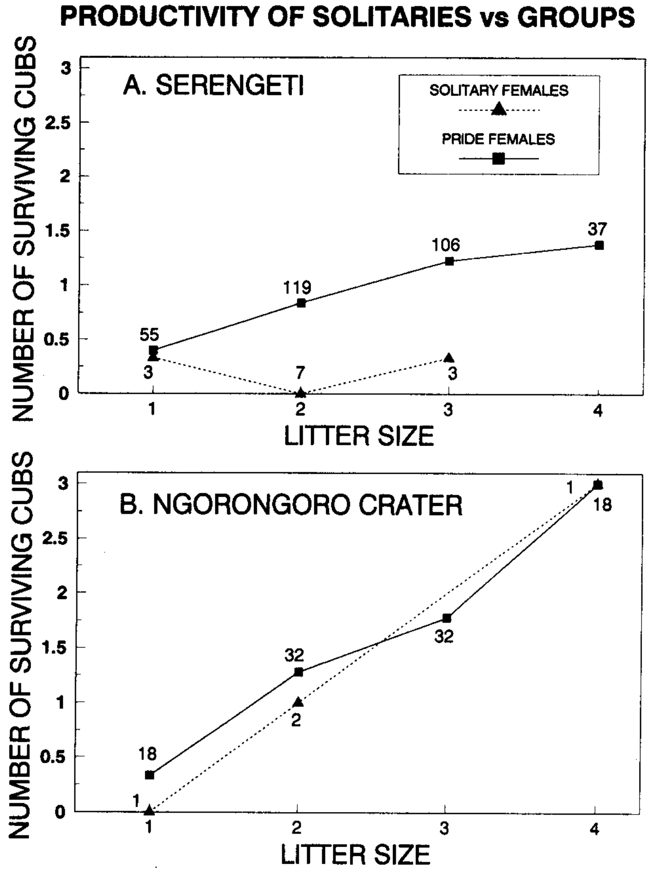

FIG. 3.—Productivity of different litter sizes when reared by solitary females and those living in prides in (*A*) the Serengeti and (*B*) the Ngorongoro Crater. The productivity of solitary females in the Serengeti remains constant with increasing litter size, and for litters of two to three cubs, solitaries rear significantly fewer cubs per litter than pride-living females (Mann-Whitney, $P < .05$).

to the litter size of their companions. After separating data by habitat, the sample sizes are quite small for combinations of mothers with litters of one or four, but since females mostly give birth to litters of two or three we can test which of these two litter sizes is more likely to be evolutionarily stable.

The payoffs from the Serengeti (table 1, top portion) indicate that the optimal litter size is frequency-dependent: if all females in the population were to give birth to two cubs, the population could be invaded by females with a litter size of three. When paired with a mother of two cubs, a female with three cubs gains significantly higher fitness than does a female with two cubs. However, a female with three cubs gains significantly lower fitness when paired with another mother of three cubs than when paired with a mother of two cubs, and a population where all females gave birth to three cubs would apparently be invaded by females with two-cub litters: when companions have three cubs, females with two cubs

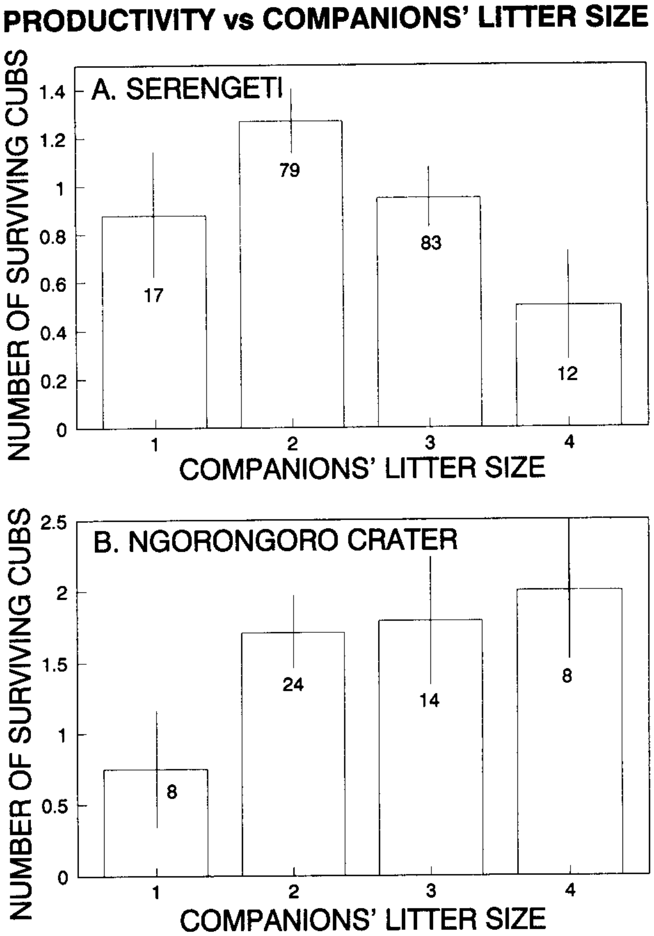

FIG. 4.—Effect of companions' litter size on the average productivity of each female's litter in (*A*) the Serengeti and (*B*) the Ngorongoro Crater. This effect is significant in the Serengeti (across companions' litter sizes of one to four: Kruskal-Wallis, $H = 9.76$, df = 3, $P = .02$; across companions' litter sizes of two to four: $H = 9.46$, df = 2, $P < .01$) and remains significant in a discrete binomial regression analysis that controls for the female's own litter size (for companions' litter sizes of two to four: coefficient:SE = $-2.40$, $P < .02$). No similar trends were found in the Ngorongoro Crater ($P > .20$ for all tests).

gain slightly higher fitness than those with three, although this last difference is not statistically significant.

Accepting these data as representative for all combinations of Serengeti mothers with two- and three-cub litters, the evolutionarily stable mixture of litter sizes is given by solving the following equation:

$$w_2 = 1.04p_2 + 1.09p_3 = w_3 = 1.79p_2 + 0.88p_3,$$

where $w_2$ is the fitness from a litter size of two, $w_3$ is the fitness from a litter size of three, $p_2$ is the proportion of females with litters of two, $p_3$ is the proportion with litters of three, and $p_3 = 1 - p_2$ and thus $p_2 = 0.22$.

TABLE 1

PAYOFF MATRICES FOR FEMALES AND THEIR PRIDEMATES THAT GAVE BIRTH WITHIN 90 d OF EACH OTHER

| FEMALE'S OWN LITTER SIZE | PRIDEMATES' AVERAGE LITTER SIZE | | | |
|---|---|---|---|---|
| | 1 | 2 | 3 | 4 |
| Serengeti: | | | | |
| 1 | .75 ± .25 (4) | .50 ± .17 (10) | .31 ± .13 (13) | .25 ± .25 (4) |
| 2 | .57 ± .30 (7) | *1.04 ± .18 (27)*$^{A}$ | *1.09 ± .15 (35)* | .60 ± .40 (5) |
| 3 | 1.00 ± 1.00 (2) | *1.79 ± .25 (28)*$^{A,B}$ | *.88 ± .22 (26)*$^{B}$ | 1.00 ± 1.00 (2) |
| 4 | 1.00 ± 1.00 (2) | 1.29 ± .40 (14) | 1.14 ± .55 (7) | N.D. |
| Ngorongoro Crater: | | | | |
| 1 | 0 (2) | .60 ± .24 (5) | 0 (2) | N.D. |
| 2 | 1.00 ± 1.00 (2) | 1.60 ± .27 (10) | 1.33 ± .42 (6) | 1.00 ± 1.00 (2) |
| 3 | 1.00 ± .71 (4) | 2.40 ± .60 (5) | 1.00 (1) | 2.00 ± .55 (5) |
| 4 | N.D. | 2.33 ± 1.20 (3) | 3.20 ± .80 (5) | 4.00 (1) |

NOTE.—Data are means ± SE, with number of litters in parentheses; N.D., no data. Paired superscripts denote cells involving two- and three-cub litters that are significantly different from each other (Mann-Whitney *U*-test, *P* ± .02).

Thus if the Serengeti data were restricted to litters of two or three, the evolutionarily stable strategy (ESS) would be a mixture of two and three cubs in an approximate ratio of 1:3.5. This analysis assumes that pridemates are unrelated to each other, but all female pridemates are close relatives (Bertram 1976; Packer et al. 1991*a*) and thus female lions would be expected to "cooperate" by more frequently giving birth to litters of two cubs—litters of two give a higher payoff against other litters of two (1.04 surviving cubs per litter) than litters of three cubs do against other litters of three (0.88 surviving cubs per litter). Following Maynard Smith's (1982, app. F) inclusive-fitness method for calculating a mixed ESS between relatives, $p_2 = 0.34$ when $r = 0.2$ (the average relatedness between adult females as estimated by Bertram [1976]). Thus a game between relatives predicts that females give birth to two- and three-cub litters in a ratio of 1:1.9, which is considerably closer to the observed ratio of 1:0.9 (fig. 1).

Although the data from Ngorongoro are too sparse to provide a comparable quantitative analysis, crater females are not affected by their companions' litter sizes (fig. 4*B*), and mothers with four-cub litters generally have the highest payoff against all litter sizes (table 1, bottom portion). Thus it is possible that both the ESS and the optimal litter size in the crater is four cubs. Nevertheless, the distribution of litter sizes in the crater is virtually identical to that in the Serengeti (fig. 1). The crater lion population is small and isolated, but it has been subject to periodic gene flow from the Serengeti (Packer et al. 1991*b*), and such gene flow may have prevented the crater lions from achieving a locally adaptive increase in litter size (as suggested for several bird species: Dhondt et al. 1990).

Besides satisfying the requirements of a mixed ESS, variation in lion litter size could also result from partial reproductive failure. However, a number of polytocous mammals exhibit physiological mechanisms for maintaining a constant litter size (Birney and Baird 1985), and partial failure appears to be rare in lions (Smuts et al. 1978). The observed proportion of small litters is higher than predicted by our game-theoretic analysis for the Serengeti, and although this could partly result from a low level of partial reproductive failure, the excess of small litters could also be due to the fact that females must sometimes raise their cubs alone. The optimal litter size for lone mothers appears to be smaller than for communal mothers (fig. 3*A*), and even pride-living females must rear their cubs alone when they give birth asynchronously.

Game-theoretic aspects of litter size may be widespread in mammals: nonoffspring nursing is common in a wide variety of polytocous species, and polytocous females typically give birth to a distribution of litter sizes (Packer et al. 1992). Even in passerine birds, the productivity of an individual's clutch may be influenced by the clutch sizes of its neighbors insofar as increased clutch sizes produce greater feeding competition between neighboring families.

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