NOTES AND COMMENTS

INTRASEXUAL COOPERATION AND THE SEX RATIO
IN AFRICAN LIONS

In spatially structured populations, sex ratios are expected to deviate from equality to favor the more productive sex. Most sex-ratio models emphasize the diminishing returns of producing more of one sex than of the other through the effects of local mate competition or local resource competition (Hamilton 1967; Clark 1978; Charnov 1982; Clutton-Brock et al. 1982; Maynard Smith 1985). Production of one sex may be favored, however, when there is local resource enhancement through cooperation by individuals of that sex (Clark 1978; Emlen et al. 1986). Although there is considerable empirical evidence that local mate competition leads to female-biased sex ratios in Hymenoptera (see reviews in Charnov 1982; Herre 1985), there is much less evidence that reproductive enhancement affects the sex ratio (Gowaty and Lennartz 1985). We show here that African lions bias their sex ratios in favor of males when those males enhance each other's expected reproductive success.

Lions in the Serengeti National Park and Ngorongoro Crater, Tanzania, live in stable social groups, and the reproductive success of individuals of each sex depends on the number of like-sexed companions that they have. Males form coalitions of up to seven individuals that act as a unit in competition against other coalitions. A successful coalition gains temporary, exclusive access to a group of females ("pride") for up to several years before being ousted by another coalition. Larger coalitions are more likely to gain residence in a pride, remain in residence longer, and gain access to more females than do small coalitions; coalition partners appear to have similar mating success (Bygott et al. 1979; Packer et al., in press). The success of larger coalitions is sufficiently high that the per capita lifetime reproductive success of males increases strikingly with increasing coalition size. Females live in prides of 1–18 adult females, all females of the pride breed at a similar rate, and females in prides of 3–10 adult females have higher individual fitness than those in larger or smaller prides (Packer et al., in press).

The probability of living in a large group as an adult depends primarily on the size of the cohort in which an individual was reared. Females of a pride that give birth synchronously pool their young and rear cohorts of young communally (Schaller 1972; Rudnai 1974; Bertram 1975; Packer 1986). "Cohort" refers to cubs
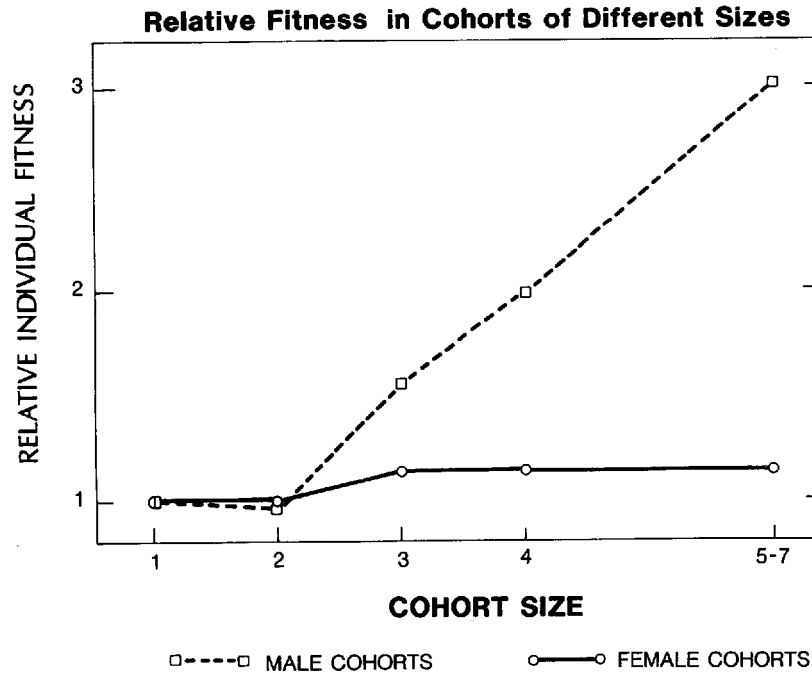
Relative Fitness in Cohorts of Different Sizes

Fig. 1.—The relative fitness of individual males and females in cohorts of like-sexed companions. Male fitness is based on the proportion of males in each cohort size that became members of coalitions of 1–7 males multiplied by the expected per capita lifetime reproductive success in coalitions of those respective sizes (given in Packer et al., in press). Cohorts of 1 or 2 males may be enlarged after dispersal to become coalitions of 2 or 3 males (see the text), whereas some cohorts of 6 or more males break up, and a proportion of these become resident as coalitions of 3 or 4 males. Female fitness is based on the proportion of females in each cohort size that became members of prides of three different sizes (1 or 2, 3–10, more than 10 females) multiplied by the fitness of females in prides of those respective sizes (Packer et al., in press). Relative fitness in each sex is the individual fitness in each cohort size divided by the fitness of singletons of that sex. Data based on 280 males and females that reached 18 mo of age (Pusey and Packer 1987).

of the same pride that are born within 1 yr of each other. Although these cohorts contain cubs of both sexes, the sexes become segregated by about 2 yr of age. The resulting like-sexed cohorts subsequently disperse as groups or, in the case of most female cohorts, remain in the natal pride together (Hanby and Bygott 1987; Pusey and Packer 1987). Male coalitions of four or more males are always composed of males from the same cohort, although smaller coalitions often include nonrelatives (Packer and Pusey 1982; Packer 1986; Pusey and Packer 1987; Packer et al., in press). Most young females are incorporated into their mothers' pride, but about a third disperse together to form new prides (Pusey and Packer 1987).

Using data collected since 1974 on over 20 prides, we have calculated the expected fitness for males and females given the size of their like-sexed cohort at the age of dispersal (fig. 1). Whereas male fitness increases dramatically as the

TABLE 1

Sex of Cubs and Timing of Male Takeover

Days since Most Recent Takeover	Male	Female	Proportion Male	Deviation from 0.50
≤300	129	96	0.57	$\chi^2 = 4.84$, $P < 0.05$
>300	268	281	0.48	$\chi^2 = 0.31$, NS
Two-by-two $\chi^2 = 4.63$, $P < 0.05$				

Note.—Gestation takes 110 days, and the synchronous births associated with male takeovers occur in the first 300 days after the takeover (see Packer and Pusey 1983a,b). Data are from 1974–1985 and exclude 100 cubs for which we do not know the timing of birth relative to the preceding male takeover. Note that when all data are included, the overall sex ratio does not deviate significantly from equality: 50.9% male, $n = 874$, $\chi^2 = 0.29$.

cohort size increases beyond two, female fitness does not change to the same extent with increasing cohort size. Male fitness is about the same for cohorts of one and two males because singleton males almost always join up with unrelated partners and thus become members of coalitions of 2 or 3 males (data in Pusey and Packer 1987). Females in small cohorts often remain with their mothers' pride and thus reside in prides of 3–10 females. Those in cohorts containing 3 or more females are more likely to emigrate when their natal pride would exceed 10 females if they stayed. Thus, because of this dispersal pattern of females, most females live in prides of 3–10 (Pusey and Packer 1987), and female fitness remains fairly constant across female cohort sizes.

An increase in the number of males in a cohort enhances male reproductive success much more than would a comparable increase in female number on female reproductive success. Thus, sex ratios in lions should be male-biased when a large cohort could be produced within a pride. A female lion could predict that her sons would be in such a cohort in two ways. First, large cohorts occur when females give birth in synchrony with other females of their pride. Breeding is most synchronous within a pride in the first few months after a male takeover. Incoming males kill or evict all of the dependent young when they first enter the pride (Bertram 1975; Packer and Pusey 1984; Hanby and Bygott 1987), the females all return to sexual receptivity within a few days of losing those cubs, and all conceive within 190 days of the takeover; since gestation is 110 days, all females give birth within 300 days (Packer and Pusey 1983a,b). Cubs born much later into the tenure of a male coalition are less likely to be born synchronously with cubs of other females in the pride (Packer and Pusey 1983b).

Table 1 shows that the sex ratio of cubs born in the first 300 days after a male takeover does indeed significantly favor males and differs significantly from the sex ratio of cubs born subsequently. We do not know whether the male-biased sex ratio reflects a bias at birth or a postpartum adjustment by the mothers, since we cannot observe cubs until they are 3–12 wk old. Our observed litter sizes are somewhat smaller than those reported in captivity (Schaller 1972), suggesting that
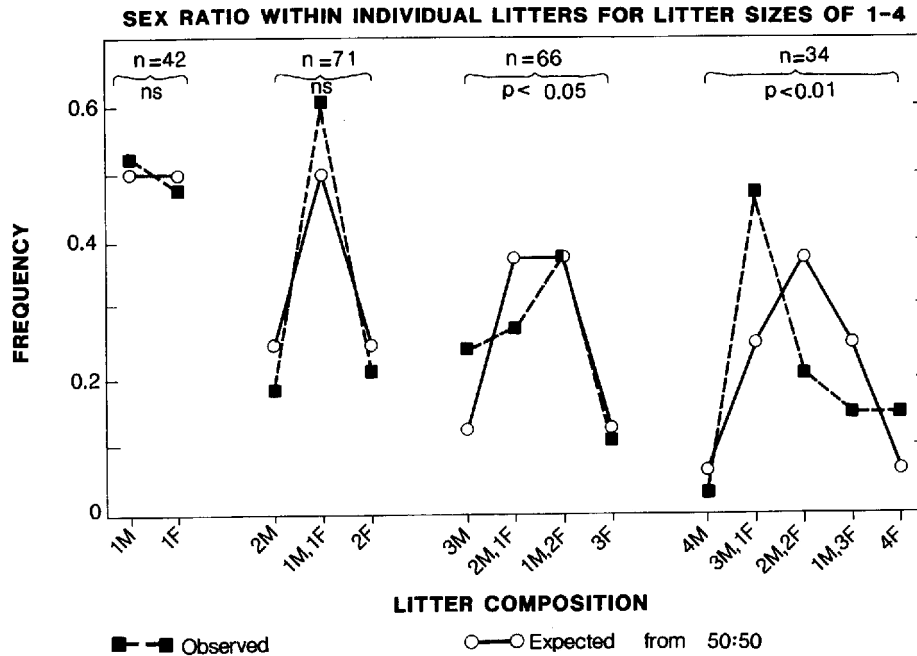
SEX RATIO WITHIN INDIVIDUAL LITTERS FOR LITTER SIZES OF 1-4

Fig. 2.—Sex ratios in litters of 1-4. Observed distributions are compared with expected values based on a binomial distribution with a 50:50 ratio of males to females. For litter size of three, $G = 7.93$, df $= 3$, $P < 0.05$; for four, $G = 13.59$, df $= 4$, $P < 0.01$. Data include only litters in which every cub could be sexed and the maternity of cubs could be assessed. Many litters are born so synchronously that it is impossible to attribute maternity and hence to discern the composition of individual litters (see Packer et al., in press).

some early mortality occurs. However, we consider postnatal elimination of daughters to be an unlikely cause of the results in table 1, since there is no detectable sex difference in mortality before 12 mo of age between cubs born within 300 days after a takeover and those born later. Regardless of how the biased sex ratio is achieved, mothers invest more reproductive effort in sons than in daughters when breeding is synchronous within the pride.

Second, a mother can predict that her sons will have at least a few male companions when her own litter size is large. Litter size in these lions ranges from 1 to 6, and 98% of litters are 1-4 ($n = 274$). Figure 2 shows that the sex ratio in litters of 3 or 4 cubs deviates significantly from a binomial distribution based on a 50:50 sex ratio, whereas the sex ratio in smaller litters does not. In both cases, the deviation from the expected distribution results from more litters containing three males than would occur by chance.

The high frequency of three males and one female in litters of four (rather than all four males) led us to examine the effects of differing litter composition on the survival of cubs of each sex. The survival of male cubs to 1 yr of age depends on the number of males in the litter. Male mortality is significantly higher in litters

with three males than in those with two males (18.2% vs. 2.9%, $n = 81$ and 34, χ^2 = 4.85, $P < 0.05$). Litters containing four males are too few to test, but by extrapolating from the increased mortality of three males, a mother would increase the number of surviving males in her litter by only 0.19 if she gave birth to four sons rather than to three. There is no comparable effect for female cubs, nor is female survival affected by the number of males in her litter. Males in litters with three males have a significantly higher chance of becoming members of cohorts of three or more than do those with only two males (58% vs. 20%, $n = 62$ and 15, $\chi^2 = 4.67$, $P < 0.05$). Therefore, the most productive composition of a litter of four is three sons and one daughter, since this yields the highest expected number of grandchildren. By a similar analysis, the most productive composition of a litter of three is three sons. Note that because pairs of male littermates have no better chance of becoming members of cohorts of three or more males than do singleton males, there is no advantage to producing two males in a litter of two. Also note that litter sizes do not vary significantly at different times after a takeover, and thus the data in table 1 are not merely the result of consistently larger litters in the first 300 days after a male takeover.

Again, we cannot be certain whether these biases are due to postnatal infanticide by the mother or to a bias in the sex ratio at birth. In armadillos of the genus *Dasypus*, mitosis takes place twice in the zygote before blastocyst formation, resulting in identical quadruplets (McBee and Baker 1982). An intriguing possibility in the lions is that male zygotes may sometimes divide to form two or three identical brothers. We are currently investigating blood samples from the lions to determine whether male littermates are more likely to be genetically identical twins or triplets than are females. The only trio of male uterine siblings so far examined appears to be composed of a pair of identical twins and a fraternal sibling (J. S. Martenson and S. J. O'Brien, pers. comm.).

The fitness function in figure 1 is based on empirical data and thus shows the payoffs to individual males and females given the actual behavior of the population. This function allowed us to predict that the sex ratio should favor males when the resulting males would become members of a large cohort, and the data confirm these qualitative predictions. We cannot predict the evolutionarily stable sex ratio, however, because we cannot estimate accurately the effects on relative individual fitness of varying levels of male-male competition. Cohorts of six or more males are often unable to remain together as a coalition long enough to take over a new pride as a group (Pusey and Packer 1987; Packer et al., in press). With a greater male bias in the sex ratio, an increase in the intensity of male-male competition would ensue and the resulting large cohorts might be even more likely to split up. As a result, the relationship between male cohort size and individual fitness might become an inverse-U-shaped function.

Circumstances leading to a biased sex ratio in haplodiploid organisms generally result in dramatic deviations from equality, whereas in animals with a chromosomal sex-determination system the deviations tend to be small (Charnov 1982; Clutton-Brock and Albon 1982). Although the sex ratio in lions varies according to predictions of local mate "enhancement," these differences likewise tend to be

small. Therefore, the XX-XY system may well act as a constraint preventing larger deviations in the sex ratio in lions. However, our detailed knowledge of the consequences of grouping to each sex has enabled us to reveal significant departures from the expected mammalian norm.

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