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Egalitarianism in Female African Lions

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Because most cooperative societies are despotic, it has been difficult to test models of egalitarianism. Female African lions demonstrate a unique form of plural breeding in which companions consistently produce similar numbers of surviving offspring. Consistent with theoretical predictions from models of reproductive skew, female lions are unable to control each other's reproduction because of high costs of fighting and low access to each other's newborn cubs. A female also lacks incentives to reduce her companions' reproduction, because her own survival and reproduction depend on group territoriality and synchronous breeding. Consequently, female relationships are highly symmetrical, and female lions are "free agents" who only contribute to communal care when they have cubs of their own.

Animal societies are often characterized by disparities in female reproduction. Eusociality is defined by a system of queens and workers; many birds form groups with a single reproductive female and numerous "helpers at the nest" (*1*, *2*). Carnivore species such as canids, mongooses, and meerkats show essentially the same pattern of a dominant reproductive female attended by subordinate helpers (*3–6*). Spotted hyenas form clans with multiple breeding females, but the top-ranking female garners greater reproduction than do subordinates (*7*), a pattern found to a varying extent across nonhuman primates (*8–10*). Theoretical models have highlighted circumstances in which female-female competition can lead either to despotism or egalitarianism, but most recent empirical research has focused on species showing extreme forms of skew. However, where related taxa show an almost universal trend toward despotism (*11*), a truly egalitarian species merits close examination—especially since egalitarianism may have promoted several of the emergent properties that characterize human society (*12*, *13*).

Theoretical models predict that reproduction is most likely to be skewed where group productivity permits subordinates to tolerate a disproportionately small share of reproduction, costly dispersal reduces the opportunity to escape manipulation by dominant companions, and kinship compensates helpers through inclusive fitness effects (*14–18*). Long-term studies suggest that African lions should be strongly predisposed toward reproductive skew: Pride-living females gain higher per capita reproduction than do solitaries or pairs, dispersing subadult females suffer reduced fitness, and female pridemates are always close genetic relatives (*19–21*). Yet lion prides are well known for containing multiple breeding females (*22*, *23*).

Lions of the Serengeti National Park and Ngorongoro Crater, Tanzania, have been studied continuously since the 1960s (*22*, *24*), and this analysis includes all births between 1963 and 1999. Reproduction can take place in any month of the year; gestation is 110 days, and the interbirth interval is about 2 years (*25*). Because of the secretive nature of females around parturition, we are unable to monitor all births, but we can track every cub that reaches its first birthday. Most juvenile mortality occurs in the first year of life (*19*); thus, we use the number of yearlings as our measure of lifetime reproductive success. Maternity is known for 80% of cubs but has to be attributed to candidate females in the remaining cases [also see (*21*)]. For example, if maternity cannot be assigned for three cubs reared by two mothers in a pride of seven females, we award 1.5 cubs to each mother and 0 cubs to the other five.

To quantify the degree of reproductive skew in each pride, we compared the observed variance in lifetime reproduction across females to a distribution of 1000 simulated variances generated by the same reproductive rate and demography as the real pride but with births randomly allocated to each female (*26*). The first set of simulations only includes cubs of known maternity and thus overestimates the degree of skew by excluding a proportion of cases in which multiple females had in fact reared their cubs simultaneously. The second set uses all data, including cases of "shared maternity," and thus underestimates skew by apportioning shared cubs equally between candidate females. Testing the null hypothesis of random reproduction corresponds to testing whether the observed variance was more or less extreme than the simulated variances (P value = the proportion of simulated variances that were larger than the observed variance). Figure 1A illustrates the lifetime reproduction of individual females in a subset of eight prides: The three prides showing the lowest variances (and hence the highest degree of "evenness"), two representative prides showing intermediate evenness/skew, and the three prides showing the highest levels of skew.

The distribution of P values across all study prides is summarized in Fig. 1B. Overall, the within-pride variance in individual reproduction appears to be no greater than expected by chance. Restricting the data to cases of known maternity, only 1 of 24 prides (4.2%) showed a degree of skew that was significant ($P < 0.05$). Including all cases of inferred maternity, 3 of 31 prides (9.6%) showed higher evenness in individual reproduction than expected ($P > 0.95$). If lions showed a persistent tendency for even a partial degree of skew, there should have been an excess number of prides with P values in the 0.05 to 0.50 range, but there were about as many as would be expected if reproduction were random. The greatest case of skew occurred in a pride [TO (Fig. 1A)] where a lone female survived the death of her companions and spent most of her life as an unsuccessful solitary; the other two cases (MK and TI) resulted from the deaths of childless young females during disease outbreaks. Thus, demographic stochasticity contributes more to within-pride variation in individual reproduction than do any underlying differences in female reproductive performance.

Such egalitarianism is most likely to develop in species where one female is unable to

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control the reproduction of another (*27*, *28*), and reproductive control would be particularly difficult to maintain in lions. First, in contrast to cooperatively breeding birds and mammals that keep their young in a central nest or den (where the alpha female can easily eliminate the subordinates' offspring), female lions retain the typically catlike trait of pronounced secrecy during parturition. Lion prides are fission-fusion societies (*22*, *29*); pridemates are seldom found all together, and females are least gregarious when they first give birth, becoming relatively solitary and hiding their cubs (even from pridemates) for the first few weeks of life (Fig. 2), thus minimizing the opportunities for infanticide by potential despots. Second, the fighting ability of subordinates is expected to be a major deterrent to despotic behavior (*14–16*). Lions possess formidable weaponry, and social relationships are remarkably symmetrical: Unlike females in species with well-developed dominance relationships (*3*, *6*, *7*, *30*, *31*), female pridemates do not harass each other or assert themselves during social interactions.

Feeding is the most common context for aggressive competition in lions, but pridemates rarely supplant members of the same age-sex class, and there is no discernible feeding hierarchy among females. Instead, same-sized individuals respect each other's "ownership" of a specific feeding site at a carcass: "Owners" signal their willingness to fight by growling, snarling, and/or lunging toward any animal that moves too close to them. "Rivals" either halt or move to a different part of the carcass. Figure 3 summarizes the outcome of feeding contests within and between different age-sex classes. Adult males are the largest members of the pride, followed by adult females, subadults, yearlings, and cubs. In most comparisons, larger age-sex classes were owners as often as as they were rivals, but for males versus yearlings, males were always owners, whereas yearlings were rivals. Owners almost always win contests between members of the same age-sex class (size is considered invariant in these cases). Males dominate every other age-sex class at the kill (Fig. 3A), readily supplanting females, subadults, and cubs. In contrast, females respect the ownership of subadults, yearlings, and cubs (Fig. 3B), and females never supplanted each other from a substantial quantity of meat (*32*).

Respect of ownership defines lion etiquette [also see (*33*, *34*)], and lions learn the rules at an early age. After being kept apart from the rest of the pride for their first 6 weeks of life, litters are merged to form a persistent nursery group or crèche (*29*). Cubs nurse primarily, but not exclusively, from their own mother (*35*) and frequently attempt to displace each other from the nipple. Size confers an advantage, with larger cubs winning most encounters with smaller cubs (76%, n = 156 encounters, $P < 0.001$); but the owner wins most encounters between same-sized cubs (61%, n = 93 encounters, $P < 0.039$). Young lions also respect ownership at carcasses, with owners winning 75% of cub-cub encounters (n = 24 encounters, $P = 0.022$) and all encounters between same-aged subadults (n = 27 encounters, $P < 0.001$).

Respect of ownership arises from two factors. First, the owner of a feeding site (whether meat or milk) possesses a clear positional advantage, latching on to prey or to mother with powerful claws. Second, and perhaps most important, ownership rules are most likely to develop when the costs of fighting are high and contestants possess similar fighting abilities (*36*, *37*). The lions' extensive weaponry carries a greater risk of "mutually assured destruction" than in other social species (*34*): squabbling pridemates frequently tatter each other's ears with their claws and can even risk blinding.

Intergroup competition is a major determinant of female reproductive success; thus, pridemates are essential allies. Females vigorously defend joint territories against neighboring prides, and gang attacks can be fatal (*19*, *29*, *38*). Experimental studies show that females are highly cooperative during interpride encounters, with large prides being most willing to confront small prides and actively recruiting distant pridemates (*39–41*). Consequently, solitaries and pairs are unable to maintain stable territories, and they suffer high mortality at moderate to high population densities (Fig. 4A), where intergroup competition is especially intense (*42*, *43*). The high mortality of large prides at low and high population densities presumably reflects within-group competition, suggesting an optimal range of three to seven females per pride. Cohorts of young females generally disperse from prides that would otherwise grow too large (*20*).

Synchronous breeding greatly enhances reproductive success. Cubs enjoy increased survival when they are raised in crèches with cubs of the same age (Fig. 4B), primarily because of the greater effectiveness of multiple mothers in defending their cubs against potentially infanticidal males (*44*). These mothers are the most gregarious members of the pride (*29*, *45*), but participation in the crèche depends on having cubs of their own: If females lose their own cubs, they rapidly resume breeding and do not contribute to the care of the remaining cubs in the crèche (*25*). First-order kin are the most generous in rearing each other's young in a crèche (*35*), but mothers (for example) will not help their

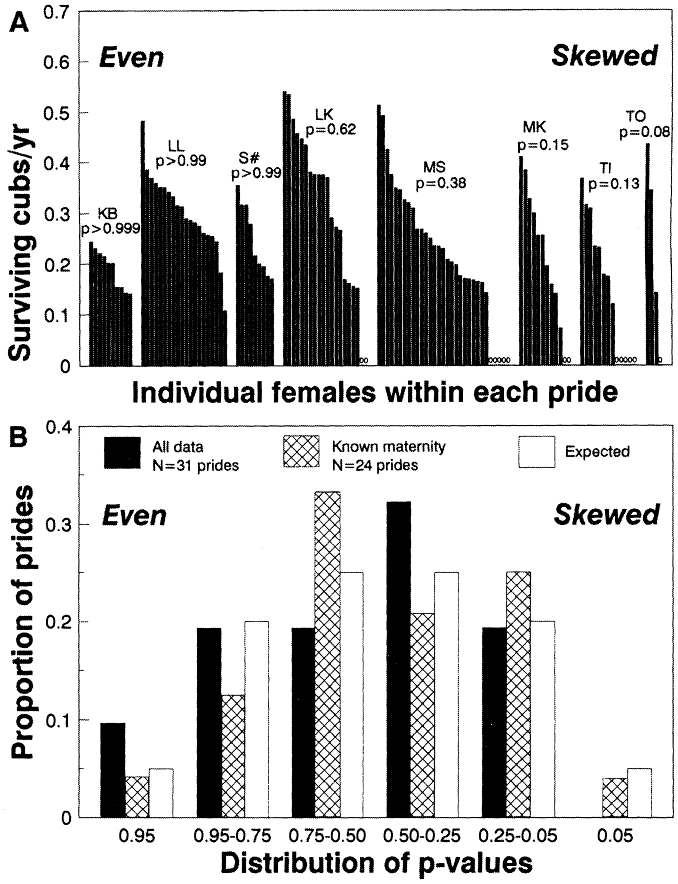
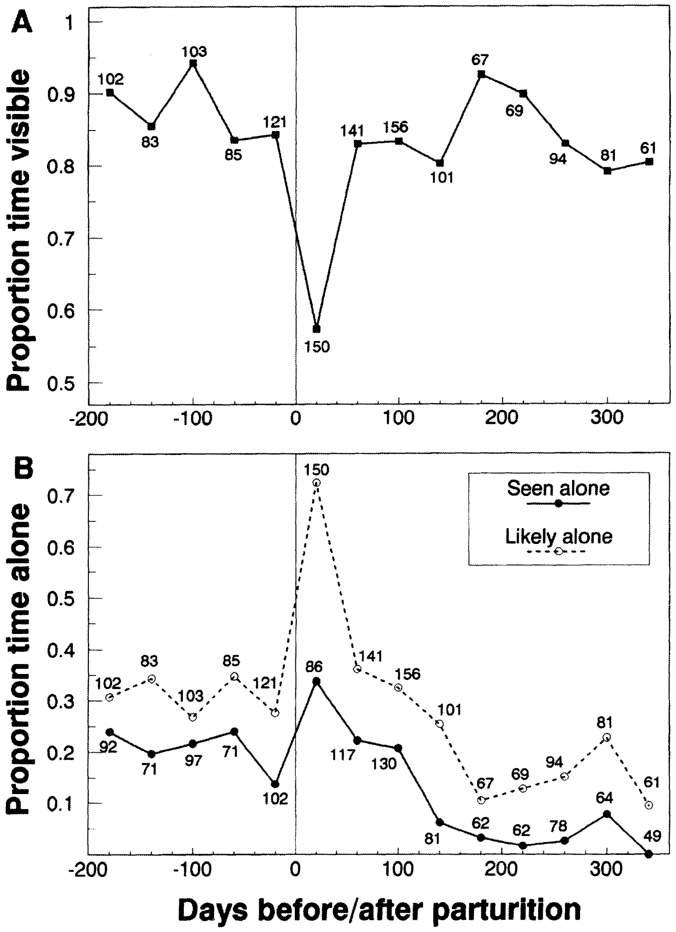


Fig. 1. Extent of reproductive skew in female lions. (**A**) Individual reproduction (the number of surviving cubs per year) in the three prides showing the highest degree of evenness (KB, LL, and S#), in two representative prides showing intermediate levels of evenness/skew (LK and MS), and in the three prides showing the highest skew (MK, TI, and TO). Nonbreeders are designated by zeroes; P values were calculated by simulation (see text). (**B**) Distribution across prides of P values for the null hypothesis of random reproduction. The observed within-pride variance in reproduction (the number of surviving cubs per female) was calculated; first, by including all data (including cubs of indeterminate parentage) (black bars), and second, using only cubs of known maternity (hatched bars). Open bars summarize the expected distribution of P values (e.g., 5% of P values should be $P \leq 0.05$, and 20% should be $0.05 < P \leq 0.25$).

Fig. 2. Changes in the behavior of radio-collared females over the reproductive cycle. Numbers refer to the total number of observations. (**A**) Females are least visible to observers during the first 40 days postpartum. Collared lions can be tracked systematically but cannot be directly observed while in dense vegetation, riverbanks, or rocky outcrops. (**B**) Time spent alone varies according to reproduction and reaches a maximum in the first few weeks postpartum. Direct observations of group composition provide a minimum estimate of time spent alone, because a hidden female is likely to be by herself. "Likely alone" assumes that hidden females are always alone.

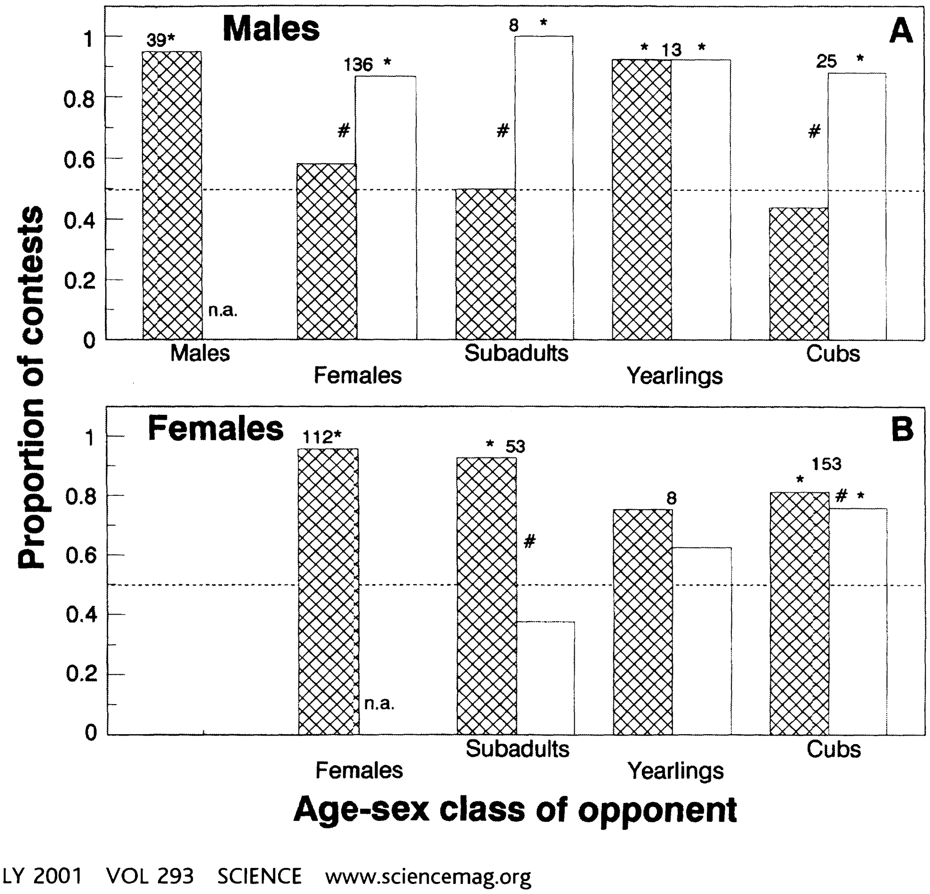


adult daughters if they do not have cubs of their own (*24*).

The advantages of cooperative cub rearing depend on synchronous breeding by multiple females. Any mutant that attempted to disrupt her companions' reproduction would thereby lose them as crèche-mates and be forced to raise her cubs alone. Synchronously breeding females gain greater per capita reproduction (Fig. 4B), and their egalitarian behavior is not vulnerable to cheating. Any female who attempted to "dump" her current litter with the crèche and then "double-clutch" would effectively orphan her first litter [orphans suffer 92% mortality (*24*)], while her second litter would be subjected to increased mortality from competition with older cubs (Fig. 4C).

Female lions gain considerable advantages from group living, but unlike other social carnivores, their reproduction is not skewed. Females form remarkably egalitarian societies that are characterized by two key features: symmetrical relationships and a voluntary system of communal cub rearing that requires active reproduction by multiple females. These two features may have evolved independently of each other, or one may have given rise to the other. A lack of social dominance is likely to have facilitated communal cub-rearing because female lions are unable to control each other's reproduction, but mutualistic benefits from crèche formation might also have

Fig. 3. Outcomes of pairwise feeding competition. Interactions are ordered according to the size of each age-sex class. The larger wins (open bars) by gaining or maintaining access to a specific region of the carcass at the expense of the smaller. "Owner" refers to a feeding individual; a "rival" attempts to gain access to the same part of the carcass. The owner wins (hatched bars) by excluding the rival; the rival wins by supplanting the owner. Asterisks indicate significant ($P < 0.01$) deviations from 50% for large versus small or owners versus rivals. (**A**) Males routinely supplant smaller age-sex classes from kills; thus, size differences are more important than ownership (marked by number signs, with $P < 0.05$ in all cases). (**B**) In interactions between females and subadults or cubs, ownership predicts outcome better than size (also marked by number signs, $P < 0.01$).



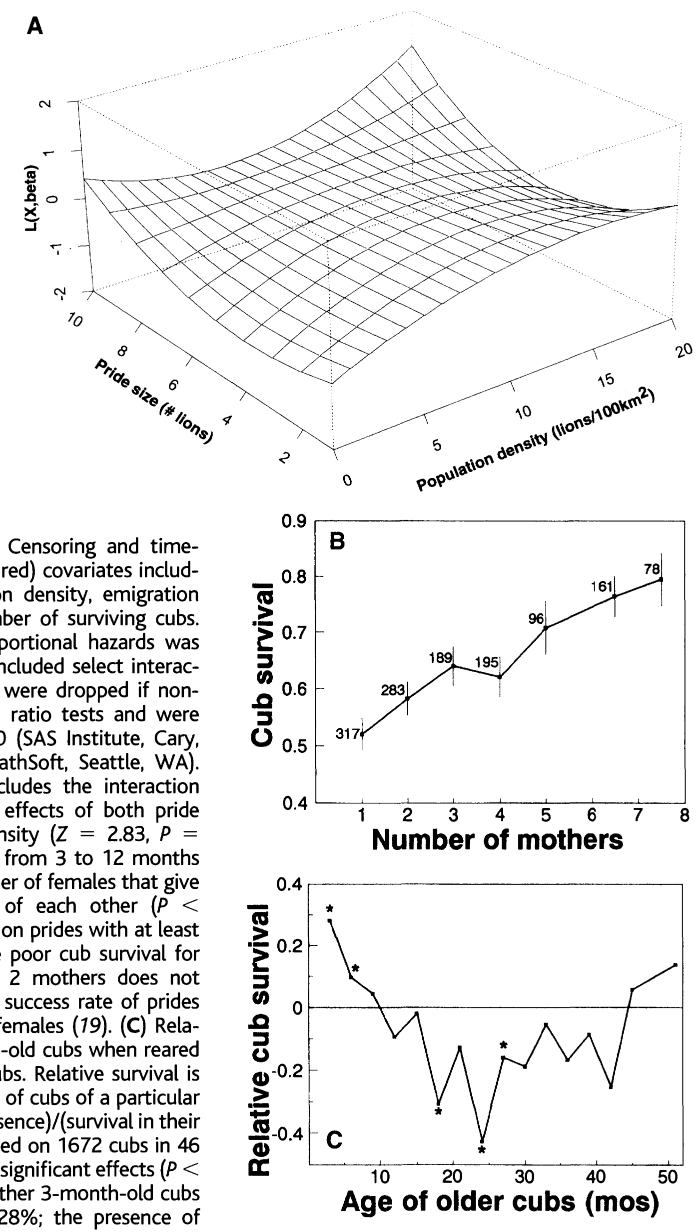


Fig. 4. Effects of grouping on female mortality and cub survival. (**A**) Predicted log of the hazard multiplier $L(X,\beta) = X\beta$ by pride size and population density. Predicted values are from the proportional hazards model (*48*) of female survival to next year, based on current pride size, population density, and number of surviving cubs. The hazard of death at age t for any individual is equal to the common hazard multiplied by an individual covariate structure: $\text{hazard}_i(t) = \text{hazard}_0(t) \times \exp(X_i\beta)$. Censoring and time-varying (annually measured) covariates included pride size, population density, emigration status, region, and number of surviving cubs. The assumption of proportional hazards was checked (*49*). Analysis included select interactions of interest, which were dropped if nonsignificant by likelihood ratio tests and were performed with SAS 8.0 (SAS Institute, Cary, NC) and S-Plus 3.4 (MathSoft, Seattle, WA). The minimal model includes the interaction between the quadratic effects of both pride size and population density ($Z = 2.83$, $P = 0.005$). (**B**) Cub survival from 3 to 12 months increases with the number of females that give birth within 1 month of each other ($P < 0.0001$). Data are based on prides with at least three females; thus, the poor cub survival for crèches with just 1 or 2 mothers does not merely reflect the poor success rate of prides containing only 1 or 2 females (*19*). (**C**) Relative survival of 3-month-old cubs when reared in crèches with older cubs. Relative survival is (survival in the presence of cubs of a particular age – survival in their absence)/(survival in their absence). Analysis is based on 1672 cubs in 46 prides; asterisks indicate significant effects ($P < 0.05$). The presence of other 3-month-old cubs raises cub survival by 28%; the presence of 24-month-old subadults reduces cub survival by 42%.

reduced incentives to form strong dominance hierarchies: The "winner" of a damaging fight not only risks personal injury (*16*) but also risks incapacitating a valuable companion (*46*, *47*). In any case, lion society provides a distinct alternative to the dog/bird model of cooperative breeding and reveals the female lion to be one of nature's few true democrats.

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