MATTERS ARISING

Coalitions of male lions: making the best of a bad job?

BYGOTT *ET AL.*[1] present data from lions (*Panthera leo* L.) showing that coalitions of males are more likely to gain tenure of female prides, retain tenure longer and produce more total offspring than singletons. These results are the first confirmation from field studies that cooperation within groups enhances reproductive success and thus that such cooperation increases the fitness of the individuals involved.

I would like to point out an important feature of Bygott *et al.*'s data which clarifies exactly how an individual male lion gains when joining a reproductive coalition rather than when gaining tenure of a pride himself. Bygott *et al.*'s conclusion that males in coalitions of three or more gain significant reproductive advantages is derived by multiplying the expected reproductive success of males in coalitions of different size by the probability of different-sized coalitions gaining tenure of prides. This calculation results in a single combined measure of reproductive success which increases with increasing group size (see Fig. 1 in ref. 1).

However, there are at least two distinct ways in which individual male lions might gain by joining coalitions: first, males might enjoy a direct benefit, probably due to the more efficient foraging made possible by hunting with other males. Second, the advantage might be only indirect, due to ecological conditions 'forcing' individuals to form coalitions to gain access to a crucial resource[2,3].

The data presented by Bygott *et al.* can be readily separated in order to address this issue. From their Fig. 1, the estimated total number of offspring fathered by males during the average tenure of coalitions of different sizes can be obtained (Table 1). These values are lowest for pairs and singletons and highest for coalitions of three to six. Assuming, as do Bygott *et al.*, no skew in male reproductive success, the number of offspring per male is readily derived; this value is greatest for singletons (Table 1). If skew in male reproductive success occurs, the expected reproductive success for all but the dominant male in groups is likely to be lower than these mean values. As a singleton can expect to produce more offspring during his tenure than the average member of a coalition, individual male lions do not seem to gain directly by joining coalitions. However, data from Table 1 of Bygott *et al.* clearly show that the probability of gaining tenure of a pride is high for coalitions of three or more, but low for singletons and pairs. Clearly, if prides were not limiting, the optimal strategy for males would be to breed as singletons. Thus, the advantage to males in coalitions is indirect, due to the greater probability of obtaining access to a female pride. This conclusion is not altered by the high average relatedness among males in coalitions[4], as the gain to an individual's inclusive fitness derived through the reproductive success of related males in a coalition will not exceed that gained through independent reproduction of those same males, given that they can obtain access to a pride[5].

Table 1 Total and per male reproductive success of lions during the average tenure of coalitions

No. of males in group	Total reproductive success	Reproductive success per male
1	8	8
2	4	2
3	14	4.7
4	10	2.5
6	30	5

Data from ref. 1, Fig. 1.

The distinction is important to understanding the evolution of group living. Any male able to gain tenure over and hold a pride by himself should do so; forming coalitions is favourable only when ecological conditions result in severe competition for breeding opportunities among males. In such conditions, males that are unsuccessful at holding a pride themselves are forced to accept the (relatively) inferior alternative of joining a coalition to obtain any breeding opportunity in the population. Thus, forming coalitions may be a conditional strategy evolved among males, many of which would be unsuccessful at gaining tenure of a pride on their own, for 'making the best of a bad job'[6]. This does not imply that coalitions need be composed of males that have themselves tried unsuccessfully to gain tenure of a pride on their own, but only that such a conditional strategy might have evolved on an evolutionary time scale.

Bygott *et al.* ask, "If members of large groups generally enjoy higher reproductive success, why do not all male lions form large coalitions?". This is a serious problem, because less than half (45%) of males in their study were found in large coalitions of three or more. Their explanation of this discrepancy, based on the low reproductive rate of lions and the difficulty of forming coalitions, is unlikely, because if males in large coalitions enjoy direct reproductive advantages there should be strong selection to overcome problems of group formation and to form large coalitions, even if they include unrelated males. However, viewed with the perspective proposed above, this paradox is resolved: any male that can obtain tenure by himself should do so, and coalitions will only be as large as is necessary to ensure that individual males are likely to be able to gain tenure of a pride.

Maynard Smith and Ridpath[7] have discussed an analogous situation—that of mate sharing by males in the Tasmanian native hen *Tribonyx mortierii*. Males were found to have higher individual reproductive success as singletons than when sharing a mate with another male, usually a sibling. The authors concluded that the evolution of cooperative polyandry in this species depended on females being a limiting resource. In these conditions, cooperation among males is again parsimoniously explainable as a conditional strategy forced on males failing to obtain a female on their own.

A similar argument attributing group formation to ecological conditions forcing individuals to form coalitions (habitat saturation[8] or resource localization[2,5]) rather than to direct reproductive advantages resulting from group living can be applied to many other group-breeding birds, in which *per capita* reproductive success of individuals in groups is lower than, or at best no higher than, that of pairs[5,9]. Of these group-living vertebrates, however, the most complete evidence on the relative importance of these advantages is that presented by Bygott *et al.* on lions. Those data strongly suggest that male coalitions cannot be explained by any intrinsic advantage to living and cooperating in groups, but rather as making the best of ecological circumstances which force some individuals to form coalitions to gain any sort of breeding opportunity.

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