

therefore, from a few decades in the  $\beta = 10^{-1}$  case to a few weeks when  $\beta = 10^{-4}$ .

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## Parent–offspring conflict

SIR — Emlen and Wrege<sup>1</sup> describe a nice example of agreement between the behaviour of bee-eaters and parent–offspring conflict (POC) theory. But additional interpretations may be plausible. Of the 47 observed attempts at harassment, only 17 were by parents of the victims. Because this fraction is low, one might ask whether the situation described has originated and been maintained by selection directly for parental exploitation of offspring or by another route.

More apparent from the data is conflict between older and younger individuals, or generation conflict. Age alone explains more harassment (72%) than parent–offspring relatedness alone (36%). The fact that male offspring are sometimes harassed by their parents could be no more than a byproduct of harassment by breeders of younger individuals in their territorial group that attempt breeding. Harassers were said to have “preferentially selected close genetic kin as targets”, but this result seems to occur mainly from the delayed dispersal of sons and the fact that sons are necessarily younger than their fathers.

The benefit to a parent from a son who helps it after abandoning its own breeding effort would then be a simple consequence of delayed dispersal by sons, indiscriminate harassment of some younger breeders, and the tendency of sons to help parents. Because older individuals are assumed to be dominant over younger ones, an alternative hypothesis, dominant–subordinate conflict (DSC), is indistinguishable from generational conflict in this case. Harassed males were more likely to become helpers than unharassed males, but this observation is consistent with parent–offspring, generational and dominant–subordinate hypotheses, given the delayed dispersal of sons.

Because 24–31% of successful recruitment attempts reported in ref. 1 did not involve a parent and its offspring, it is clear that recruitment of non-offspring can be effective and that the generational and dominant–subordinate hypotheses would also ‘explain’ the behaviour of harassers by generating benefits.

By invoking selection theory, Emlen and Wrege have, perhaps unintentionally, implied that the intolerance shown by breeding bee-eaters towards sons has been increased and maintained by natural selection. In the avian context, however, the norm is for parents to exclude offspring totally from breeding on the parental territory. It follows, therefore, that the situation in bee-eaters constitutes a reduction in aggressiveness of fathers towards sons rather than an increase. A yearling paired male has a 74% chance of not having its nesting attempt disrupted (59% if parents present). Thus, although bee-eater parents do harass a few offspring, among others, this may be part of a general intolerance by dominants of subordinates who share their resources, and it may have arisen through increased tolerance of offspring rather than increased harassment of them, as has been suggested using parental-facilitation theory for New World jays<sup>2</sup>. This theory accommodates both the facilitation of breeding by some offspring and the harassment of others.

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EMLEN AND WREGE REPLY — Virtually all cooperatively breeding species exhibit familial social organizations in which grown offspring delay dispersal and remain with their parents. This is generally considered to be the necessary precursor for the evolution of helping<sup>2–5</sup>. Thus we agree that bee-eaters show increased parental ‘tolerance’ of offspring when contrasted with nonhelping species. But the question we addressed was not the origin of families, but the separate issue of the social dynamics of individuals living within families.

Cases of breeding harassment and suppression are commonplace within family-structured animal societies. Our goal<sup>1</sup> was to offer a framework for examining such familial conflicts and their resolutions based upon kinship. Brown offers an alternative framework based upon age and dominance.

Kinship and dominance undoubtedly have additive effects upon recruitment. Our data, however, refute the hypothesis that age/dominance is the primary influence, in that we reported<sup>1</sup> a significant tendency for harassing bee-eaters nonrandomly to target close kin as the subjects of their harassment. Perhaps we

did not state clearly enough that this analysis was restricted to harassment patterns within extended family groups and only to equal aged or younger family members. We have now repeated this analysis including only younger family members. In this test, a wide array of kin of differing degrees of relatedness are potentially available as targets, but all are younger than, and presumably subordinate to, their harassers. The results are the same, confirming that harassers are not “indiscriminate” in their interactions with younger family members, but preferentially harass those to whom they are most closely related.

The costs of ‘yielding’ to harassment explain this pattern. Targeted individuals that are unrelated will gain little from becoming helpers and are predicted to exhibit greater resistance (as demonstrated<sup>1</sup>). Selection will then favour an ability of harassers to focus their efforts on those individuals likely to resist the least — namely close kin.

Parent–offspring conflict theory is merely a subset of inclusive fitness theory<sup>6</sup>. We did not mean to imply that father–son interactions have been moulded by selection pressures distinct from other categories of relatives. Our point was that kinship influences both the types of interactions expected with, and the amount of ‘leverage’ wielded over, others. Kinship-specific payoffs predict the pattern of harassment/recruitment found in bee-eaters. They also provide a testable framework for interpreting general patterns of reproductive conflict and suppression in all other animals that live in family-structured groups.

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