

When fathers harass their sons

Among white-fronted bee-eaters, a bird species found abundantly in east and central Africa, fathers torment their sons and physically prevent them from breeding. The sons in time abandon their efforts to start a family and return to the parental nest as helpers.

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WHEN animals live in groups, many paradoxes occur that are hard to explain within the framework of the classical Darwinian theory of natural selection. For example, a honey-bee spends its entire life working selflessly for the welfare of its queen mother and thousands of its sibling larvae.

In 1964, scientist W D Hamilton provided an elegant modification of Darwin's theory of natural selection that helps also to understand the apparent paradoxes of social life. Hamilton's theory of inclusive fitness contends that organisms do not merely maximise their individual fitness (a function of the number of their own children) but they maximise their inclusive fitness (a function of the number of their own children and also the number of their genetic relatives — brother and sister bees — whom they help). An interesting consequence of this concept is that more inclusive fitness may potentially be gained by raising large numbers of genetic relatives, instead of bearing one's own children. The beauty of this theory is that it permits a simple calculation of how many brothers and sisters need to be raised to compensate for a certain number of children given up.

An offspring contributes more to the inclusive fitness of the parent by helping the parent than by breeding on its own.

Perhaps an even more bizarre consequence of group living is seen in white-fronted bee-eaters (*Merops bullockoides*), which are common birds of the savannas of east and central Africa. These birds breed gregariously in large colonies of

about 200 individuals. In about half the nests, the parents get help in rearing chicks, usually from an older son who has been unable to start his own family.

Apparently, adult sons aren't able to start their own families because they are actively harassed by their own fathers who are still breeding on their own. Some might wonder whether this interpretation of this behaviour of these birds is not too anthropomorphic. But their behaviour, as described after years of study by Stephen T Emlen and Peter H Wrege of Cornell University in USA, is unmistakable. The fathers persistently chase their harassed sons away from their territory. Furthermore, they interfere with the courtship of their sons by preventing them from feeding their consorts and position themselves in front of the nest and physically prevent them from entering the nest. A frequent consequence of such



A white-fronted bee-eater, with a bee tucked in its beak, is perched on a twig.

behaviour is that the sons abandon their attempts to raise a family and return to the father's nest and act as helpers.

Why do fathers harass their sons and why do the sons **47**

succumb to such harassment? Why do fathers choose their sons as targets of harassment? Why is the highest success in recruiting helpers achieved by the fathers through harassing their sons?

These apparent paradoxes are not difficult to understand within the framework of the inclusive fitness theory. Emlen and Wrege marked individual white-fronted bee-eaters and followed them over many years. They are thus in a unique position to compute the costs and benefits of such harassments in terms of inclusive fitness. Breeders without helpers fare very poorly but the presence of helpers proportionately increases breeding success. Hence, an offspring contributes more to the inclusive fitness of the parent by helping the parent than by breeding on its own.

From the point of view of the parent, the benefit of harassment (in terms of more children produced), is much greater than the cost (in terms of grandchildren

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lost). From the point of view of the sons, it turns out that their inclusive fitness by having their own families is roughly the same as what they would obtain if they helped their parents. So, it's because the cost to the sons (in terms of children not reared) and the benefits (in terms of siblings reared) of succumbing to harassment are almost identical, that the sons fail to register any strong desire to resist parental harassment. By contrast, unrelated individuals even when harassed are less likely to become helpers in their harassers' nest. This makes sense, because unrelated individuals would not be rearing siblings but unrelated chicks, should they become helpers. As such, the benefit to them would be much less than the cost. ■

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