Reprinted from *Current Science*, Vol. 59, No. 9, 10 May, 1990, pp. 445 - 446

Nepotistic bee-eaters

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Darwin's theory of natural selection which is often described rather dramatically as 'survival of the fittest' expects animals to behave in a selfish manner towards all other individuals except their own offspring. There are however several tantalizing examples of behaviours among animals that may be termed *altruistic*—the most striking of these are several instances of 'helpers' among insects, birds and mammals that temporarily or permanently forego their own reproduction and help other members of their species reproduce. The most important conceptual advance in our attempt to explain such 'paradoxical' behaviour came in 1964 with Hamilton's theory of *kin selection* or *inclusive fitness*[1]. The central idea of this theory is that fitness comes not only from rearing one's own offspring but may also come from caring for one's genetic relatives. In other words, altruistic behaviour is not paradoxical if it is also *nepotistic*, i.e. directed preferentially towards genetic relatives.

Although the relevant mathematics of computing fitness by including an individual's contribution to the survival and reproduction of relatives was rapidly perfected, the theory of kin selection (which claims that animals maximize their inclusive fitness), like the theory of natural selection itself is not easy to falsify. This difficulty is best illustrated by the variety of hypotheses that have been put forward to explain the evolution of helping behaviour in birds. In many species of birds such as the Florida scrub jay (*Aphelocoma coerulescens*)[2], the Galapagos mocking bird (*Nesomimus parvulus*)[3], the jungle babbler (*Turdoides striatus*)[4], the acorn woodpecker (*Melanerpes formicivorus*)[5], the Pied Kingfisher (*Ceryle rudis*)[6], the splendid wren (*Malurus splendens*)[7] and the white-fronted bee-eater (*Merops bullockoides*)[8], some individuals postpone breeding and help other breeding pairs of their species in the often difficult task of rearing chicks. Typically, helpers contribute to feeding the chicks, feeding the parents as well as guarding the nest. The obvious question is why should helpers help? Studies of many species with such helpers have shown that the strategy of postponing reproduction and acting as a helper can have profound consequences both for the helpers and for those that are helped. The phenomenon of helpers in birds thus provides a convenient arena to test the theory of kin selection. The theory of kin selection may be considered validated if it can be demonstrated that helpers help only because they gain fitness through the indirect effect of their help to their genetic relatives and not because helping somehow also enhances their own personal probabilities of survival and reproduction.

This is just the kind of proof of the theory of kin selection that Emlen and Wrege[9] provide in a recent paper on the white-fronted bee-eater. Emlen and Wrege sexed (by laparotomy, because the sexes cannot be identified externally), individually marked (with leg bands and coloured patagial tags) and intensively observed a large population of white-fronted bee-eaters for five years in Lake Nakuru in Kenya. During these studies, they found that the white-fronted bee-eater which is a close relative of our very common small green bee-eater (*Merops orientalis*), lives in extended family units or clans and that in each breeding season numerous clans aggregate to form large colonies of about 200 birds each. About 50% of all nests have at least one non-breeding helper that participates in excavating and defending the nest, feeding the breeding female before she lays eggs, incubating the eggs and feeding the nestlings and fledglings. Every year, Emlen and Wrege painstakingly recorded, for every nest, the number of helpers, the identity of the breeders and that of the helpers, the clutch size, hatching success and fledgling success. In addition, they have been able to determine the genetic relatedness between the helpers and the helped.

With such data, Emlen and Wrege have been able to test nine different hypotheses that have been proposed for how helpers might benefit from helping. These hypotheses may be broadly classified into four classes: (i) helpers have a better chance of survival if they associate themselves with a nest, (ii) by helping, helpers increase their probability of becoming breeders in the future, (iii) helpers are more successful at breeding if they have had past experience as helpers, and (iv) helpers gain fitness indirectly through helping genetic relatives. Notice that the first three classes of hypotheses depend on direct benefit to helpers and evidence in support of any of these would not permit us to accept the theory of kin selection. Emlen and Wrege find no evidence that an individual increases the chances of its survival by being a helper nor do they find that helpers are more likely to become breeders in the future. If they do become breeders, they are not significantly more successful than those without prior experience as helpers. However, helpers significantly increase survival of the nestlings and help only when they are rather closely related to the nestlings[8]. In other words, there is clear evidence against the first three classes of hypotheses and equally clear evidence in favour of the fourth class of hypotheses. Using a 'kin index' developed by Vehrencamp[10], they show that helping behaviour in the white-fronted bee-eater is entirely altruistic in that the fitness gained by a helper is exclusively due to the indirect effect of helping close relatives. Taken together, the results of this study provide compelling evidence for the role of kin selection in shaping animal behaviour.

When Hamilton first developed the ideas of inclusive fitness and kin selection, it appeared that if there is one group of animals where his ideas will definitely work, it is the honeybee and its relatives in the insect order Hymenoptera. In social insects such as ants, bees and wasps (all belong to the order Hymenoptera), there is a curious genetic system known as haplodiploidy which potentially makes some genetic relatives even more closely related than offspring so that it should be 'easier' to gain fitness through aiding relatives than it is by rearing offspring. Although kin selection may still be a significant factor, it appears that haplodiploidy, which makes kin selection especially plausible, may not hold the key to the evolution of sociality in the Hymenoptera after all[11]. But Emlen and Wrege's study on white-fronted bee-eaters comes as good news for kin selectionists—if not the bees then at least the bee-eaters!

Note. Terms such as 'altruism', 'nepotism', etc are routinely used in studies of animal behaviour and evolutionary biology merely for the sake of convenience. However, they are objectively defined in terms of the consequences for the biological fitness of the actors and recipients of behavioural acts and should by no means be construed as having any moral connotation that is inevitable when the same terms are used in the human context.

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