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In Focus

Featured Articles in This Month's *Animal Behaviour*

Why Woodpeckers Help

One of the greatest problems in evolutionary biology is why natural selection sometimes leads to the evolution of cooperative traits such as helping. Biologists use the term 'helping' to refer to behaviour in which individuals care for young that are not their own offspring. In birds and mammals in which helping occurs, young that are helped are typically relatives of the helpers, often their younger sibs or half-sibs. Helpers then reap an 'indirect' fitness benefit from their actions, meaning that they increase the frequency of their genes in future generations by enhancing the success of individuals that are not their direct descendants but that none the less share their genes. Helping may also have 'direct' benefits, that is, the behaviour may somehow increase the helper's own survival or reproduction. Although kin selection theory has firmly established the evolutionary logic of the indirect benefits mechanism, some biologists have taken the view that evolution through direct benefits is a more parsimonious hypothesis, so that the importance of indirect benefits in the evolution of behaviours such as helping can be accepted only if all possible direct benefits are disproven. Accordingly, it is of great interest that a study in this issue (pp. 437–444), by Walter D. Koenig and Eric L. Walters, carefully tests two possible direct benefits of helping in the cooperatively breeding acorn woodpecker.

Acorn woodpeckers have an unusually complex breeding system for a vertebrate, with multiple adults of both sexes breeding together on a single territory (Fig. 1). Helpers are additional, nonbreeding adults, and are almost always offspring of one or more of the breeders. Helpers have been shown to enhance the reproductive success and survival of breeders, so helping does have an indirect benefit.

Koenig and Walters use a very long-term data set (1979–2010) from their study population in central California to test two hypotheses on direct benefits of helping. The first hypothesis is that, by helping, young birds gain skills that benefit them when they eventually become breeders. One prediction of this 'skills hypothesis' is that young birds lacking experience should perform relatively poorly in breeding activities. In support of this prediction, the authors found that rates at which helpers provided food for young increased with the age of the helper, at least when comparing the youngest age classes. A second prediction, however, failed: individuals that helped more as nonbreeders did not have greater success in producing young in their first year as breeders than individuals that helped less.

A second, rather cynical hypothesis is that helpers help as a sort of bribe to the breeders, to induce the breeders not to expel them from the communal territory. This 'pay-to-stay' hypothesis predicts that individuals that help more should end up remaining on the

Figure 1. Five members of a cooperatively breeding group of acorn woodpeckers at the authors' study site on the Hastings Reservation in central California. Photo: Bruce Lyon.

territory for longer, which Koenig and Walters found to be true for male helpers in their study population, although not for female helpers. Consequently, males that helped more in their first year of helping were more likely to inherit the territory than were males that helped less. This last result could occur just because the

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probability of inheriting increases with age, and indeed when Koenig and Walters compared the age-specific probability of inheritance for pairs of broodmates, males that helped more were no more likely to inherit than males that helped less.

Koenig and Walters conclude that their data do not support direct benefits to helping through either a skills or a pay-to-stay mechanism. Although it is always possible that additional data will change the picture, these authors are already able to bring a truly impressive long-term data set to bear on the question. One is forced to conclude that these two direct benefits, at least, are unlikely to be important in this case, which in turn increases our confidence that indirect benefits are central to the evolution of helping in this cooperatively breeding species.

William A. Searcy
Executive Editor

Alternative Mating Strategies in Elephant Seals

Elephant seals are a model species for our understanding of animal mating strategies because they have extremely polygynous sexual behaviour. In polygynous mating systems a male mates with many females while a female mates with one male. Polygyny is common in mammals because females provide parental care and their reproductive success is limited by resources while the reproductive success of males, who contribute only gametes, is limited by the number of mates. Hence a patchy distribution of resources could lead to a clustered distribution of females and extreme competition between males for access to them. Under such competition, the alternative male strategies of fighting and sneaking to gain mates have been predicted and demonstrated. By contrast, until very recently, alternative female strategies have been overlooked, mainly because of the theoretical prediction that choosing dominant fighting males who can protect a resource is adaptive for females. There is evidence, however, that in polygynous mating systems females are harassed by males. Therefore, it is difficult to distinguish between female choice and male coercion arising from male–male competition. Long-term data on individually recognizable animals is needed to elucidate the possibility of alternative female mating strategies.

In the present issue (pp. 445–451), Nico de Bruyn, Cheryl Tosh, Marthán Bester (University of Pretoria, South Africa), Elissa Cameron (University of Pretoria and University of Tasmania, Australia), Trevor McIntyre (University of Pretoria) and Ian Wilkinson (New South Wales Office of Environment and Heritage, Australia) reveal fascinating results from a 25-year study of southern elephant seals on the sub-Antarctic Marion Island (Fig. 2). Females of the southern elephant seal come ashore for a maximum of 6 weeks per year to give birth and then mate. They show fidelity to such 'haul out' sites apparently because of their limited availability. This results in female aggregations and intense male–male competition, associated with increased harassment of females by males, including the separation of pups from mothers, which in turn apparently increases female aggregation to reduce such harassment. The female to male ratio at haul out sites is between 9:1 and 277:1 and the dominant male is responsible for around 50–70% of paternities. However, up to 75% of the adult male population is at sea during the mating season and there is evidence that females experience their first mating at sea. This suggests that both sexes employ nonterrestrial, alternative mating strategies.

The authors assessed 3689 individual breeding histories of 15 cohorts of adult female southern elephant seals from all 54 haul out beaches on Marion Island over 25 breeding seasons (1983–2007). All females were born on the island and were marked immediately after weaning with individually specific tags on their hindflippers (a well-established technique which has been shown not to have any deleterious long-term effects). All seals were checked for identification and breeding status at least every 7 days during the breeding season from 1983 to 2007 and statistical detectability analysis demonstrates that there was less than 4% chance of missing a female with this method if she was present.

The results of this study provide evidence that females mate out at sea. They do not return to the island and to a polygynous mating system every year and do not need to haul out on land in order to mate. These results are based on the 1032 adult females (or 28% of those tagged at weaning) who returned at least once to the island and to a polygynous mating system within the 25-year observation period. Of the 794 females who participated in more than one breeding haul out on the island, 80% did not return for at least one season. Of these, 69% gave birth and at a maximum 11% only mated on their return to the island after such a missed breeding haul out. Since conception occurs 1 year before a female gives birth, such a high percentage of births without a haul out on the island for more than a year is evidence that a substantial proportion of females and males mate at sea. It strongly suggests that alternative nonpolygynous opportunistic mating at sea may be an important alternative strategy in what, up to now, has been regarded as an extremely polygynous mating system. Intriguingly, de Bruyn and coauthors present the sea tracks of two individuals whose movements were fortuitously followed during a skipped breeding season as part of tracking 53 females equipped with satellite-linked devices (which are known not to affect individual mass gain and long-term survival) during 1999–2009. Both tracks imply that the females mated at sea.

This study suggests that nonpregnant female southern elephant seals might benefit more from continued foraging and encountering males, without being harassed, on an opportunistic basis at sea than from being in an aggressively competitive polygynous system at haul outs. This calls for similar re-evaluations of polygynous mating systems to be undertaken in other species. The authors show not only the importance of looking at variation in both female and male mating strategies but also the value of considering behavioural variation in individually recognizable animals over long periods in general.

Ana Sendova-Franks
Executive Editor

Figure 2. Southern elephant seals at one of the sites studied by the authors on Marion Island. Photo: Nico de Bruyn.