Eusociality, life underground and parasites

In their recent review, Wcislo and Danforth[1] provided evidence of a secondary loss of social behaviour in halictid and apid bees. Their unorthodox view may help to illuminate the evolution of social behaviour in other organisms or will, at least, provide a new stimulus for discussion.

One of their conclusions was that the maintenance of eusocial behaviour might be too costly because of an increased likelihood of disease and parasite transmission. However, very little was said about this in the reference[2] cited by the authors to support their argument. It would be interesting to know what the evidence really is for increased risks of being parasitized in eusocial bees compared with their solitary relatives.

Recently, we have shown[3] that very similar arguments to those of Wcislo and Danforth may also apply to the evolution of sociality (or solitariness) in African bathyergid mole-rats (*Cryptomys* and *Heliophobius*). We examined the incidence of parasites in the eusocial *Cryptomys* genus[4]. As pointed out by Alexander *et al.*[2], most eusocial forms live in the soil and these mole-rats are no exception. The ecotope is humid and warm[5] and, combined with social behaviour (such as close contact, communal toilets and coprophagy), would be expected to favour diseases and parasites. However, compared with some above-ground and burrowing small mammals[6], which are usually infested by ecto- and endoparasites, *Cryptomys* species are virtually ectoparasite-free and are much less infested with helminths (usually only with the nematode *Protospirura muricola*)[4]. Although the related, but solitary, silvery mole-rat, *Heliophobius*, seems to be even less infected than *Cryptomys* (A. Scharff and H. Burda, unpublished), the blind mole-rat, *Spalax ehrenbergi*, which is also solitary and subterranean, shows high infestation rates with nematodes[7].

These data are confusing. On the one hand, the data on bathyergids suggest that the subterranean lifestyle reduces the likelihood of parasitic infections and that this risk is further lowered by a solitary lifestyle; this would support the hypothesis of Wcislo and Danforth[1]. On the other hand, *Spalax* infestation rates do not differ from those of other small rodents. Unfortunately, because there are still too few comparative data and very little is known about the life cycles and requirements of helminth parasites, these inconsistencies and, therefore, the relationship between parasites, the subterranean way of life and social behaviour in mole-rats will remain unexplained.

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Reply from W.T. Wcislo and B.N. Danforth

We are grateful to Drs Scharff and Burda for bringing to the attention of readers the proceedings of a recent conference that have bearing on evolutionary gain or loss of social behavior. Our review[1] examined the phylogenetic patterns of halictid and apid bees, to assess the assumption that social behavior is always derived. In some lineages, this assumption is not supported; social behavior can be lost, thus giving rise to secondarily solitary species. According to Scharff and Burda, a similar phenomenon occurs in naked mole-rats.

Naked mole-rats are the only vertebrate examples of caste-based societies[2] and, therefore, provide excellent opportunities for comparative studies with social invertebrates. The findings by Scharff and Burda now open the door for fascinating comparative studies on the evolutionary loss of social behavior in vertebrates and invertebrates and should help us better understand such convergent evolutionary changes.

Our review concentrated on phylogenetic patterns. We did not aim to thoroughly review the costs and benefits associated with group living or solitary behavior. In fact, our discussion of proximate mechanisms focussed mainly on patterns of seasonality. In our final paragraph, we speculated that social living is, presumably, expensive to maintain if group-living facilitates disease transmission among genetically related individuals. Scharff and Burda point out that there is little evidence for this hypothesis in the cited reference by Alexander *et al.* (and references therein)[3]. We agree that there is a dearth of data and acknowledge that Alexander *et al.* only briefly mention the costs of sociality. In an earlier publication, Alexander[4] lists automatic costs associated with group living, including 'increased likelihood of disease and parasite transmission'. A paper by Hamilton[5] might have been a more appropriate recent citation because it thoroughly discusses proposed relationships between parasitism rates and sociality (although there is still very little empirical evidence).

Scharff and Burda have found evidence indicating that solitary mole-rats (*Heliophobius*) are less infested by parasitic helminths than the social mole-rat, *Cryptomys*, and we look forward to reading their published work. Like them, we think that there 'are still too few comparative data' to understand the role of parasites and pathogens in shaping the expression of social behavior. Other factors besides disease transmission may also help account for evolutionary reversals in social behavior. We lack sufficient data to assess these factors and hope that others are stimulated to conduct further studies.

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The major transitions in evolution: what has driven them?

John Maynard Smith and Eörs Szathmáry (JMSES), in their milestone book[1], present a fascinating theoretical view of the various steps in evolution that resulted in the major transitions such as the emergence of chromosomes, of eukaryotes, of sex, of multicellular organisms, of social groups, etc. JMSES emphasize that although their book is speculative, the major transitions 'must be explained in a way that is consistent with a general theory of evolutionary change, the theory of evolution by natural selection'. They do this by showing for each major transition the likely properties that had ensured the persistence and the further development of the new structures (that is, why selection did not wipe them out). As for how the transitions originated, JMSES emphasize that 'our thesis is that the increase (in complexity) has depended on a small number of major transitions in the way in which genetic information is transmitted between generations.' Furthermore: 'there is no reason to regard the unique transitions as the inevitable result of some general law: one can imagine that life might have got stuck at the prokaryote or at the protist stage of evolution'.

The above quotations demonstrate the reluctance of JMSES to extend speculation beyond