The strange case of the naked mole-rat

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I am concerned here with some animal unknown to me. That is possible. True, I have observed the life down here long and carefully enough, but the world is full of diversity and is never wanting in painful surprises. Yet it cannot be a single animal, it must be a whole swarm that has suddenly fallen upon my domain, a huge swarm of little creatures.

Franz Kafka, *The Burrow*

Naked mole-rats (*Heterocephalus glaber*) are virtually hairless and sightless mammals (family Bathyergidae) that live in large subterranean colonies in arid regions of Kenya, Ethiopia and Somalia in eastern Africa. These 'saber-toothed sausages' (anonymous) are particularly interesting because they are eusocial: within a colony, usually consisting of about 25 to sometimes even more than 295 individuals, only one female and her one to three mates reproduce, while the young from previous litters maintain and defend the colony as well as assist in rearing newborns as do workers in colonies of the social insects.

One of the most interesting aspects of the social biology of the naked mole-rat centres around its colony organisation and the factors which maintain it. Although the mean intra-colony genetic relatedness is high (0.81 ± 0.10 for four wild-caught colonies) due to extensive inbreeding in this species[1], evolutionary conflicts of interest may nevertheless arise between the queen and her non-reproducing workers over how active the latter should be in the performance of work for the colony and the brood. A high-ranking worker could be considered a 'hopeful reproductive'[2] and therefore predicted to be lazy, since this could potentially reduce its energy expenditure, thereby increasing its probability of becoming a future breeder over its more industrious fellow workers. This is bound to increase its fitness since it will always be more related to its own offspring than to those of another worker's. In this species, relatively large or rapidly-growing individuals appear more likely to acquire and maintain breeding status[3], while workers less related to the queen have less to gain by working for her. One could thus predict that both these classes of individuals would be relatively lazy. The queen, in contrast, benefits maximally if all her workers are active, because she is also more related to her own offspring than to those of any other worker's, and worker activity would benefit her young.

In a recent interesting paper, Hudson K. Reeve provides compelling evidence for exactly this kind of queen–worker conflict[4]. The queen mole-rat appears to exercise control over the activity levels of her lazier workers by aggressive 'shoving' in which she violently pushes (and occasionally bites) a worker into exhibiting a variety of behaviours, including digging, chewing of the substrate, sweeping debris or carrying food or nesting material. True to prediction, data from six laboratory colonies show that such inherently inactive workers not only tend to be larger, but also less related to the queen than are infrequently-shoved, smaller, but industrious, workers. Interestingly, the recipients of the queen's shoves actually increase their work activity about two-fold. In addition, Reeve shows that the removal of the queen selectively depresses the activity of workers that are larger and less related to her, but (and here is an important point) only in 'satiated' colonies, i.e. colonies deprived of food for only 0–5 hours. Queen removal, however, had no significant effect on the mean work level in 'hungry' colonies deprived of food for 40–50 hours. Finally, when the queen was removed from satiated colonies, the mean relatedness to the queen of active workers increased, whereas the mean weight of the active workers decreased.

From these data, Reeve concludes that the naked mole-rat queen may indeed be in conflict with her larger, less-related colony mates over how much work these individuals should do, and possibly activates these individuals through her shoving. He further points out that the extent of queen–worker conflict may be highly context-specific, and it may not be prudent to classify animal societies as cooperative or conflictual without examining the particular social context. When the colony is hungry, for example, it is in everyone's selfish interest to search for food and the conflict thus disappears. Under conditions of satiation, however, with lowered risks of starvation, workers can pursue selfish reproductive options by being lazy.

The most remarkable aspect of Reeve's work lies in its clear demonstration of a significant positive correlation between the activity levels of workers and their genetic relatedness to the queen, and by extension, to the brood that they rear, albeit under conditions of satiation. This is a point that has always been assumed to be a corollary to the theory of inclusive fitness, but, as far as I know, never conclusively demonstrated in any study of social animals so far. It is surprising that after decades of research with social insects, it is one of the newest entrants to this field, and a mammal at that, which provides the first direct evidence to such an important caveat.

One intriguing aspect of naked mole-rat society concerns the mechanism(s) by which the queen and the three males maintain their exclusive reproductive monopoly. The differences between breeding and non-breeding mole-rats do not lie merely in behaviour, but also have physiological manifestations. Non-breeding females, for example, have only non-maturing follicles in their ovaries, and consequently, do not ovulate[3]. Moreover, they also fail to produce measurable levels of gonadotropic-releasing hormone, thus failing to trigger ovarian development[5]. How are such developmental processes inhibited?

Queen-derived pheromones have often been suggested to play a role in repro-

ductive suppression of the workers, though never proven[5]. It has also been speculated that stress caused by physical aggression shown by the queen may inhibit the release of reproductive hormones in subordinate colony members[5]. If this is indeed so, can the shoving behaviour of the queen towards her larger and less-related workers, described by Reeve, mediate such an effect? This probably cannot be completely ruled out as yet, although the lack of sex bias in the queen's shoving, and the fact that she frequently shoves her mates, may argue against it.

Yet another important question that arises from Reeve's work is whether the larger workers are indeed averse to exposing themselves to predators, as he expects them to be. In course of his field work, Stanton Braude had discovered that the largest non-breeding workers, who were previously thought only to defend the colony against predators or other naked mole-rats, often expose themselves to the greatest danger[6]. In their burrowing, naked mole-rats get rid of excess dirt in their tunnels by forming a chain in which several workers successively kick the soil behind them toward a surface-hole in the burrow. The final mole-rat in this sequence then kicks the dirt out in what has been called 'volcanoing'. Braude observed that larger workers often occupied that dangerous position. In fact, when such an animal falls prey to a snake, it gives a cry before getting killed alerting other colony members, who then rush forward and immediately seal off the passage to the predator. If this constitutes a regular feature of the behavioural repertoire of the larger workers, it may be necessary to question once more the motivations that have been ascribed to such individuals.

There is obviously much more to be discovered about the enigmatic naked mole-rat. And this is only the beginning. If these early studies of this unusual animal are any indication of what the future holds for us, we can possibly look forward to many more years of Kafkaesque surprise and wonder.

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COMMENTARY

Support for science in India

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The most disturbing feature in Indian science during the last couple of years has been the precipitous fall in governmental support to science in terms of the quantum of funds and also in terms of the perceived importance the political leadership attaches to science. It has been reported that the investment in Research and Development in India has fallen during the last few years from 1.1 to 0.89 per cent of the Gross National Product (GNP), while it is 2 to 3 per cent in developed countries[1]. This has very adversely affected research activities in most institutions in India.

The importance of scientific and technological research in a nation's life is well recognized. Development has been almost synonymous to progress in science and technology. Even in a less advanced country like India, the positive impact of science and technology has been all pervasive. Perhaps the contribution of science and technology to the development of India has not been as good as we might have wished, but it has been very significant in many areas such as those pertaining to food, industry, defence, communications, medicine, etc. Science and technology go together and it is the synergism of the two that make development possible. At a time when all who matter swear by the rapid development of the country, it is ironic, and indeed disastrous, that support for science and technology should fall so precipitously.

The cut in support for science could not have come at a worse time. During the eighties, the support for science in India, though meagre by western standards, has been on the upswing and it has been effectively made use of by many. Indeed, in many fields, we have just about turned the