Behavioural ecology: **Naked mole-rats on the move**

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The discovery of a disperser morph in naked mole-rat colonies has revealed the first possible outbreeding mechanism for this unusual mammal, and provides another remarkable parallel to the eusocial insects.

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In the 1970s, R.D. Alexander attempted to explain the apparent absence of eusociality in vertebrates by describing a mythical creature with all the traits needed for eusociality: probably a rodent, it would live a cooperative existence constructing an expandable nest in a safe subterranean environment, exploiting a large, almost risk-free food source [1]. Unknown to Alexander at the time, he had given an almost perfect description of the naked mole-rat (*Heterocephalus glaber*). These bizarre creatures, bathyergid rodents found in Africa, are in many ways more like social insects than like mammals. Virtually hairless and poikilothermic, naked mole-rats live in colonies of around 80 individuals which work cooperatively to excavate a massive network of burrows [2]. Like social insects, naked mole-rats exhibit the characteristics necessary for eusociality: reproductive division of labour, overlapping generations and cooperative care of young [3].

Each naked mole-rat colony contains only one reproductive queen (rarely two) and a handful of reproductive males; the rest of the colony are non-breeding workers, reproductively suppressed by the queen. Within the non-breeding workforce, division of labour is based on size, with smaller animals specializing in colony maintenance tasks and larger individuals specializing in digging and colony defence. Because the division of labour is based on body size, individuals can change specialization as they age and grow [2,3].

A new study by O'Riain, Jarvis and Faulkes [4] describes a previously unknown caste in some naked mole-rat colonies: the disperser. Big, fat, lazy and sexually-charged, these rare individuals seem built for dispersal. Dispersers actively seek to leave their natal burrow whenever an opportunity for escape presents itself, and are armed with generous fat reserves to survive the journey. They are sexually primed, with high levels of lutenizing hormone, yet are only interested in mating with individuals from foreign colonies, not their own colony's queen. Furthermore, they are lazy, showing little interest in working cooperatively in their natal burrow. So the disperser morphs seem perfectly equipped for leaving their natal burrow, joining another colony and thus promoting exchange of individuals, and therefore genes, between otherwise isolated colonies.

As well as providing fascinating evidence for further division of labour in naked mole-rat colonies, once again mirroring castes in eusocial insect colonies (such as winged dispersers in termite colonies [4]), the discovery of the disperser morph may shed light on a riddle in naked mole-rat biology: how can they survive intensive inbreeding? At any given time, all young born to the colony have the same mother, and there are only a few potential fathers [3]. Furthermore, because juveniles generally remain in their natal nest, there is a high level of relatedness between members of a colony, so the breeders are all close relatives. There is almost no movement of individuals between colonies, and naked mole-rats are actively xenophobic, reacting aggressively to members of other colonies. New colonies are assumed to form by fission of existing groups, and so will be genetically similar to the parent colony. Lack of dispersal and the small number of breeding individuals create a small effective population size, which reduces genetic variation in the colony [5]. Two colony mates are genetically more similar than full sibs in outbred populations; in fact, they could only be more similar if they were monozygotic twins [2].

Observations of both captive and wild populations indicate that inbreeding is a widespread problem for mammal populations [6,7]. Inbreeding causes a loss of fitness, known as inbreeding depression, due to the expression of deleterious effects in a variety of traits [7]. Inbreeding depression

Figure 1

A naked mole-rat (*Heterocephalus glaber*).

is most commonly attributed to the loss of heterozygosity. Inbreeding increases the chance of an individual getting two copies of any given allele, so rare recessive deleterious alleles, previously carried unexpressed in heterozygous individuals, are more likely to occur in the harmful homozygous state in inbred lines. Loss of heterosis, the fitness advantage of having heterozygous loci, might also contribute to inbreeding depression, although the extent and importance of heterosis in the genome is unknown.

Inbred lines may also lack between-locus genetic diversity: rather than the loss of diversity of alleles at any given locus, it may be the loss of variable combinations of homozygous loci that is manifest in inbreeding depression [8]. The deleterious effect of inbreeding may lessen over time as recessive deleterious alleles are removed by selection against homozygotes: harmful alleles are purged from the population by the death of homozygote carriers, and there are few heterozygotes to promulgate recessive alleles. This could lessen the effects of inbreeding over time and may explain the range of responses of different populations to inbreeding [9].

Despite potentially diminishing effects, inbreeding depression can exact a high enough cost to prompt the evolution of inbreeding avoidance mechanisms, such as dispersal from the family group, extra-pair and extra-group matings, recognition and avoidance of kin as mates, and delayed maturation of offspring in the presence of their parents. The occurrence of these mechanisms has been demonstrated for a range of mammals [6]. Naked mole-rats are an anomaly. With 85 % of matings occurring between parent and offspring or between siblings [2], they are the only mammal species that has been shown to undergo continuous close inbreeding, with no obvious effects of inbreeding depression.

The disperser morph seems to be adapted to outbreeding, following a common pattern of recognition and avoidance of their own queen for a mate, willingness to mate with members of other colonies and active attempts to leave the natal burrow, presumably to join other colonies (where they may be accepted as breeders if a resident breeding male has died). Even with dispersers, naked mole-rats remain the most inbred mammal known to biologists. Dispersers are rare [4], and neighbouring colonies are so genetically similar that influx of genetic variation must be limited [10]. Naked mole-rats are, for the most part, xenophobic and incestuous. But the significance of the discovery of dispersers is that if they are specially adapted for outbreeding, it indicates that, inbred as they are and almost entirely lacking in genetic variation, even naked mole-rats have their limits.

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