Family values: group dynamics and social control of reproduction in African mole-rats

Chris G. Faulkes and Nigel C. Bennett

To exploit ecological niches where constraints have favoured selection for group living and cooperation, both vertebrates and invertebrates have evolved elaborate social systems. In mammals, numerous divergent taxa have converged at similar solutions to these ecological challenges (such as food distribution and predator avoidance), culminating in the social insect-like behaviour of the naked mole-rat. Characteristically, breeding is partitioned unequally in such groups, resulting in a 'reproductive skew'. New research linking studies of physiology, behaviour and molecular ecology in African mole-rats is helping us to elucidate why different proximate mechanisms that control groups of cooperative breeders might have evolved.

Chris Faulkes*
School of Biological Sciences, Queen Mary, University of London, Mile End Road, London, UK E1 4NS.
*e-mail: c.g.faulkes@qmw.ac.uk

Nigel Bennett
Dept of Zoology and Entomology, University of Pretoria, Pretoria 0002, South Africa.

A characteristic of COOPERATIVELY BREEDING mammals (see Glossary), where individuals other than the parents help care for offspring, is that reproduction is partitioned unequally among members of the social group (REPRODUCTIVE SKEW), with socially dominant individuals monopolizing breeding opportunities. An increasing body of work is now revealing that the PROXIMATE MECHANISMS underlying this reproductive division of labour might differ between even closely related species, and debate continues about the exact role the breeding female plays in maintaining levels of reproductive skew. Theoretical models of 'incomplete control by dominants'[1] and 'concession' theory involving 'peace' and 'staying' incentives[2,3] (Box 1), have been proposed to explain inter- and intraspecific differences in reproductive skew. The idea, however, that the dominant breeder exerts, or attempts to exert, some kind of reproductive control over subordinate nonbreeders in the group is implicit in both models. This control could manifest itself in different ways, ranging from, for example, infanticide of the offspring of a subordinate, or interference by dominants with subordinate mating attempts, to actual suppression of subordinate reproductive physiology[4]. As most cooperatively breeding mammals live in extended family groups, in many cases, INCEST AVOIDANCE alone could be argued to be sufficient to maintain reproductive skew, if the only unrelated individuals in the group are the founding parents.

Almost all animals have evolved mechanisms that prevent them from breeding with close relatives. This protects them against the fitness costs of harmful recessive traits and decreased heterozygosity that might be manifest in offspring arising from such matings[5]. As molecular genetic techniques increasingly enable elucidation of the detailed kin structure of social groups, the relative roles of different proximate mechanisms that control reproductive skew can be properly understood. When does 'SELF RESTRAINT' in the form of incest avoidance give way to the more extreme DOMINANT CONTROL that could be manifest as the suppression of reproductive physiology in nonbreeders, or even infanticide of their offspring should they breed? Are there common mechanisms mediating physiological suppression among divergent taxa, such as rodents, viverrids, canids and primates[6] (Table 1), and how might ecological factors influence the proximate control of reproductive skew?

Monopoly of reproduction in African mole-rats

The African mole-rats of the family Bathyergidae are an ideal taxonomic group with which to tackle questions about both ultimate factors and proximate mechanisms that control reproduction in a social species, because they have a range of cooperative breeding strategies and differing degrees of reproductive skew. Mating preferences encompass both facultative INBREEDING and obligate outbreeding, and result in clear differences between mole-rat species in the way their social systems are maintained.

Sociality in African mole-rats

Of the 18 or more species of African mole-rats, four are solitary. The other species in the genera *Cryptomys* and *Heterocephalus* exhibit varying degrees of sociality and cooperative breeding. A characteristic feature of the social species is a reproductive division of labour, resulting in high reproductive skew and, consequently, large variation in the lifetime reproductive success of individuals. Two species, the naked mole-rat (*Heterocephalus glaber*) and the Damaraland mole-rat (*Cryptomys damarensis*), fit the classic definition of EUSOCIALITY derived from social insects[7,8]. Other mole-rats and cooperatively breeding vertebrates might also fit this definition[9,10]. Unlike other species, both Damaraland and naked mole-rats exhibit a behavioural division of labour among the nonbreeding helpers. In the Damaraland mole-rats, smaller individuals form a 'frequent worker' group, and in naked mole-rats, the frequency of 'work' in the form of 'colony maintenance' behaviour shows a negative correlation with increasing body mass[11,12]. In addition,

http://tree.trends.com 0169–5347/01/$ – see front matter PII: S0169-5347(01)02116-4

Box 1. Reproduction in cooperative breeders – hegemony versus anarchy

In vertebrates, groups of cooperative breeders are characterized by a reproductive division of labour in which a small number or, in the extreme, a single member of each sex, breed. The remaining group members, of both sexes, fulfil a 'helper' role, the nature of which varies between species. Although they are nonbreeding, these individuals might accrue indirect or inclusive fitness benefits because they are usually close relatives of the breeders. Ecological constraints are ultimately thought to provide the selective pressure for these reproductive and behavioural divisions of labour. Theories of optimal reproductive skew consider such societies as a continuum of social systems, which differ in the way that lifetime reproductive success is distributed among group members on a scale from zero to one, the so-called 'eusociality continuum'. This assumes that dominant members of the society control reproduction among the subordinates[a–d]. In 'low skew' societies, all individuals have a more or less equal chance of reproduction, whereas, in 'high skew' societies, reproduction is limited to one or a small number of individuals of each sex.

Although few would dispute that maintaining the optimal degree of skew (how many and which particular individuals breed) in a cooperatively breeding society is adaptive, there are conflicting ideas about how such reproductive division of labour is established and maintained. 'Concession' models argue that in certain circumstances it might pay the dominant individual to allow some subordinates to breed, as an inducement to stay in the group and cooperate peacefully ('staying incentives') or to prevent subordinates fighting for reproductive control ('peace incentives')[b,d]. Conversely, 'incomplete control' models suggest that subordinates breed simply because the dominant is unable to effectively suppress their reproduction[e], and 'threat of eviction' models argue that skew arises from subordinate restraint, to avoid ejection from the social group[f].

References

a Keller, L. and Reeve, H.K. (1994) Partitioning of reproduction in animal societies. *Trends Ecol. Evol.* 9, 98–102

b Reeve, H.K. *et al.* (1998) Reproductive sharing in animal societies: reproductive incentives or incomplete control by dominant breeders? *Behav. Ecol.* 9, 267–278

c Sherman, P.W. *et al.* (1995) The eusociality continuum. *Behav. Ecol.* 6, 102–108

d Reeve, H.K. (2000) A transactional theory of within-group conflict. *Am. Nat.* 155, 365–382

e Clutton-Brock, T.H. (1998) Reproductive skew, concessions and limited control. *Trends Ecol. Evol.* 13, 288–292

f Johnson, R.A. and Cant, M.A. (1999) Reproductive skew and the threat of eviction: a new perspective. *Proc. R. Soc. London B Biol. Sci.* 266, 275–279

there is solid evidence for the existence of morphologically distinct castes in naked mole-rats, including a disperser morph among males[13,14], and differences in the vertebrae of the breeding queen[15]. The ARIDITY FOOD DISTRIBUTION HYPOTHESIS proposes that eusociality and cooperative breeding in African mole-rats could have evolved in response to rainfall patterns, its effects on food distribution and the subsequent costs and risks of foraging and dispersal[16,17].

Mating system and reproductive skew

All cooperatively breeding mole-rats studied to date have skewed reproduction, with a single female normally breeding with one, but perhaps on occasion two or three, males. However, in terms of lifetime reproductive success, skew might differ considerably between species. Plural breeding in females appears to be rare[9]. The social mole-rats studied to date in the genus *Cryptomys* all have a mating system that involves obligate outbreeding, whereas naked mole-rats are unusual within the Bathyergidae and among mammals in general because they can inbreed to a high degree. These incestuous tendencies were originally proposed as an important factor in explaining their eusociality[18], and it was argued that inbreeding produced a within kin-group genetic structure analogous to haplodiploidy in the Hymenoptera. Indeed, naked mole-rats can inbreed to such an extent that intra-colony relatedness has been estimated in some groups at 0.8 (Ref. 18), greater than the maximum three-quarter relatedness possible in haplodiploid organisms where the queen is singly mated[19].

Although the inclusive fitness benefits of high relatedness to nonbreeding colony members are readily apparent, the puzzle remains that field data from other cooperatively breeding mammals, including other social mole-rat species and the eusocial Damaraland mole-rat, follow the typical pattern of incest avoidance. Thus, it has been proposed that inbreeding might be a derived trait, peculiar to the naked mole-rat, which might have evolved as an adaptive response to the high costs of dispersal. Once deleterious recessive traits were purged from a population, inbreeders would have had an advantage over obligate outbreeders, who could potentially suffer fitness costs if opportunities for finding unrelated mates were rare. Indeed, without incestuous mating, colonies in which a breeder dies could face extinction before sufficient (unpredictable) rainfall facilitates emigration. Although the propensity for naked mole-rats to inbreed, together with genetic studies of wild-caught colonies, indicate that dispersal is rare[18,20], new field and laboratory data suggest that if the opportunity arises, even in naked mole-rats, outbreeding might be the preferred mating system[14,21,22]. However, the fact that naked mole-rats will quite readily inbreed presents a problem for the queen: how can she maintain her reproductive monopoly and control over the colony when colony members will potentially breed with each other? The answer could lie in the extreme control the queen imposes on the reproductive physiology of both sexes of her socially subordinate colony mates.

Reproductive suppression in mole-rats

Naked mole-rats (Fig. 1a) represent the pinnacle of not only mammalian cooperative breeding but also of socially induced infertility. Nonbreeders of both sexes within colonies are physiologically suppressed by the queen. In females, ovarian cyclicity and ovulation are blocked, whereas in males, most nonbreeders have spermatozoa within the reproductive tract that are both reduced in number and lack normal levels of motility. In both sexes, reduced secretion of the pituitary gonadotrophin, luteinizing hormone, is evident. These extreme (but reversible) reproductive blocks are brought about by social contact with the dominant breeding

Table 1. A summary of the social and reproductive characteristics of six species of African mole-rats, compared with selected other cooperatively breeding mammals

Species	No. breeders per group (mean/max. group sizes)[a]	Role of helpers	Incest avoidance	Suppression of reproductive physiology in nonbreeders		Refs
				Males	**Females**	
Naked mole-rats						
Heterocephalus glaber	1 female/1–3 males (75/295)	Foraging, defence, pup care	No	Yes	Yes	4,7,9,11
Cryptomys damarensis	1 female/1–2 males (11/41)	Foraging, defence, pup care	Yes	No	Yes	8,9,25
Cryptomys h. hottentotus	1 female/1 male (5/14)	Foraging	Yes	No	No	9,27
Cryptomys darlingi	1 female/1 male (7/9)	Foraging	Yes	No	No	9
Cryptomys anselli	1 female/1 male (–/20)	Foraging	Yes	No	No	30,41
Cryptomys mechowi	1 female/1 male (5/11)	Foraging	Yes	No	No	9,42,43[b]
Other cooperatively breeding mammals						
Dwarf mongoose (*Helogale parvula*)	1 female/1 male (mean: 9+ up to 15 young)	Antipredator behaviour, care of young	No	No	Yes	35,37,38
Meerkats (*Suricata suricatta*)	1 female/1 male (range: 2–27)	Antipredator behaviour, care of young	Yes	No	Yes	44–46
Common marmosets (*Callithrix jacchus*)	1 female/1 male (range: 3–15)	Infant carrying	Yes	No	Yes	6,39
Gray wolves (*Canis lupus*)	1 female/1 male (packs number up to 20)	Provision and protect young	Yes	No	No	47,48[c]
Prairie voles (*Microtus ochrogaster*)	1 female/1 male (range: 2–19)	Pup care	Yes?	No	Yes	40[c]

[a] The data in this column are based on the usual patterns of sociality observed, and deviations are known to occur in most species.

[b] Group sizes of up to 60 have been proposed for *C. mechowi*, but these are based on interviews with local hunters[43] and have not been confirmed by systematic trapping.

[c] Cooperative breeding in these taxa is widespread and has been comprehensively reviewed recently for both canids[48] and rodents[40].

queen[4], and are a classic example of a dominant control model. Thus, in a society in which a high reproductive skew and a large nonbreeding workforce is adaptive, but where there is a penchant for inbreeding, a control mechanism appears to have evolved that suppresses reproductive physiology in both sexes.

In the Damaraland mole-rat, the second mole-rat species that fits the classic definition of eusociality (but is an obligate outbreeder) a clear physiological block to reproduction is observed only in nonbreeding females[23,24]. As with the naked mole-rat, ovulation is blocked, although possibly through a different physiological mechanism operating at the level of the ovary[25]. Nonbreeding males are not physiologically suppressed in the same way as naked mole-rats; however, they do possess increased proportions of immature sperm[26]. Although the significance of these sperm abnormalities for fertility is unclear, nonbreeding males make no attempt to mate with their female colony mates, which are usually close kin, presumably as a result of an incest avoidance mechanism. This effect is so strong that both wild and captive colonies in which the breeding female has died will remain reproductively quiescent (sometimes for years) until a ‘foreign’, unrelated, individual becomes available, or dispersal/fragmentation of the colony takes place[8,9].

Endocrine studies of other species have shown that in the common mole-rat, *Cryptomys hottentotus hottentotus*, neither male nor female nonbreeders have a physiological block to reproduction[27] (Fig. 1b). Inbreeding avoidance alone appears sufficient to maintain reproductive skew within colonies that are essentially family groups. A similar situation can be observed in the Mashona mole-rat, *Cryptomys darlingi*[28] and the giant mole-rat, *Cryptomys mechowi*[29] (Table 1). In another Zambian mole-rat (probably *Cryptomys anselli*), evidence was also found for the maintenance of skew by incest avoidance alone[30].

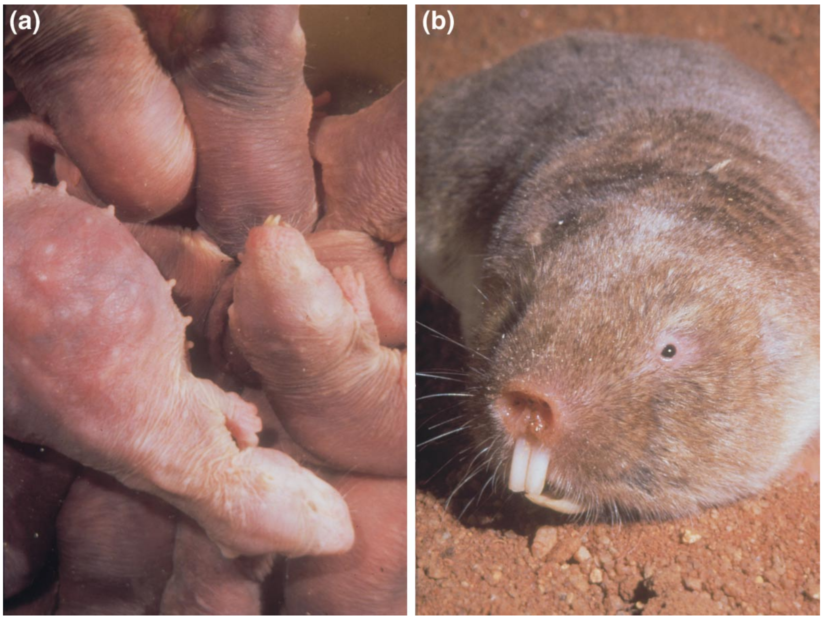

Fig. 1. From dominant control to self restraint. In the naked mole-rat *Heterocephalus glaber* (a), the reproductive physiology of both sexes is suppressed, whereas in the common mole-rat *Cryptomys hottentotus hottentotus* (b) incest avoidance mechanisms alone maintain a reproductive division of labour within colonies. *Reproduced, with permission, from Tim Jackson.*

Reproductive succession and new colony formation

New colony formation can take place in a variety of ways, even within the same species. These can

Table 2. Colony dynamics in three species of African mole-rats[a]

Species	Habitat type	Skew	Dispersal	Colony formation
Heterocephalus glaber	Semi-arid	>99%	Rare, male biased, into existing colonies	Colony fragmentation and inbreeding or outbreeding
Cryptomys damarensis	Semi-arid	*c.* 90%	Male biased, into existing colonies	Colony fragmentation and outbreeding among pairs and cohorts
Cryptomys h. hottentotus	Mesic	<90% Plural breeding at mesic sites	No sex bias: males and females can migrate into existing colonies	Colony fragmentation and outbreeding among pairs and cohorts; multiple dispersal
	Semi-arid	<90%	No sex bias, but lower rates of migration between colonies than at mesic sites	Colony fragmentation and outbreeding usually among pairs

[a]Both reproductive skew and constraints on dispersal are higher in the 'eusocial' species *Heterocephalus glaber* and *Cryptomys damarensis*. Currently, there are no accurate estimates of reproductive skew and reproductive success for *Cryptomys h. hottentotus*, but it is apparent from recent field studies that colonies show greater lability than do both *C. damarensis* and *H. glaber*, in both their mesic (high rainfall) and arid habitats. For example, in mesic habitats, 90% of colonies were shown to have different reproductive pairs on recapture, whereas at an arid site, this declined to 36%, clearly illustrating the effect of aridity on dispersal and reproductive success[16,32].

include colony fragmentation, the dispersal of individuals to form pairs and small groups, and by immigration (usually of males) into existing groups[8,31], although immigration might be rare (Table 2). Although molecular genetic studies that will enable us to fully quantify these colony dynamics are just beginning, it is clear from the field data collected so far that the more social species are characterized by a reduced turnover of breeding opportunities and new colony formation (Table 2). More than 99% of naked mole-rats never breed[16].

A long-term field study of Damaraland mole-rats has also revealed that severe ecological constraints result in around 90% of animals in a population never breeding. In the common mole-rat, a species which is generally regarded as less social, mean and maximum group sizes are smaller, there is no clear behavioural division of labour in nonbreeders, and colonies are much more labile than those of the naked and Damaraland mole-rats. Consequently, reproductive opportunities for nonbreeders are greater[32] (Table 2). Dispersal is predominantly from mixed pairs that form new colonies, rather than a sex-biased dispersal into an existing colony, although this, together with multiple dispersal by single animals, also occurs. Common mole-rats generally inhabit mesic areas, but their range can also extend into semi-arid regions. Recently, Spinks *et al.*[32] have elegantly demonstrated the influence of habitat aridity on colony dynamics in this species and shown that PHILOPATRY is greater in the harsher, semi-arid habitat. In the Mashona mole-rat and the Giant mole-rat, species that also lack physiological suppression of reproduction[28,29], little is known about dispersal patterns and lifetime reproductive success. Like the common mole-rat, these two species also inhabit areas of relatively high, predictable rainfall where ecological constraints are low, so one might predict that the chances of reproduction through dispersal and new colony formation through pairing are relatively high.

Variation in proximate control of reproduction: is there a trend in the Bathyergidae?

Comparative endocrine studies of African mole-rats suggest that the frequency and mode of dispersal and nascent colony formation, which in turn are influenced by ecological factors, might be fundamental in shaping sociality and the proximate mechanisms controlling reproductive skew in mole-rats. The functional significance of REPRODUCTIVE SUPPRESSION in male and female naked mole-rats seems to be clear, because inbreeding is possible when constraints preclude dispersal. In species such as the common, Mashona and giant mole-rats, where no physiological suppression is observed, incest avoidance alone is apparently sufficient to maintain reproductive skew because colonies might be more labile and opportunities for individual reproduction are greater.

The Damaraland mole-rat is a fascinating case because it is intermediate, with suppression of reproductive physiology in females only. One could speculate that this trait might have evolved to prevent unrelated immigrant males from mating with nonbreeding females and breaking down the social hierarchy. If this is the case, then as with the naked mole-rat, there is a dominant control model of suppression, although unlike the naked mole-rat, agonistic behaviour is uncommon. A self-restraint model, arising from the incest avoidance that is known to exist in the Damaraland mole-rat, does not explain why this species has physiological suppression of reproduction in nonbreeding females, when the other incest-avoiding social cryptomids do not (Table 1). Recent studies attempting to tease apart this enigma are equivocal and demonstrate that control of reproduction in the Damaraland mole-rat is not clear cut[33]. When captive colonies of Damaraland mole-rats with the breeding male removed were given access to unrelated males, aggression between the breeding queen and her daughters increased dramatically from being almost nonexistent. Subsequently, in 50% of

Box 2. Marmosets and tamarins

Of the 40 or so species of South American marmosets and tamarins in the family Callitrichidae, cooperative breeding strategies, where a high reproductive skew is maintained in social groups, are widespread. These small arboreal primates are unusual because they normally produce twin offspring, which at birth might have a combined mass of up to 20% of the body weight of the mother. Nonbreeders ‘help’ by adopting an infant-carrying role[a]. Perhaps the best studied of the callitrichid primates, in terms of understanding how social factors can suppress fertility, is the common marmoset, *Callithrix jacchus*. In its natural habitat of the Atlantic Coastal forests of Brazil, common marmosets live in groups of 3–15 individuals composed of an extended family with immigrants from neighbouring colonies. Reproduction in these wild groups is typically (but not always) monopolized by a single dominant female[b]. In captivity, reproductive skew in peer groups of unrelated individuals is achieved by dominant control of subordinate females.

A mixture of behavioural and pheromonal cues from the dominant female brings about a hypogonadotrophic state resulting in anovulation in females. Nonbreeding males appear to be suppressed behaviourally, rather than physiologically, by exclusion from mating[c]. In family groups studied in captivity, an interesting mix of dominant control and incest avoidance appears to operate, which is remarkably similar to the Damaraland mole-rat. In this context, 46% of daughters were shown to have ovulated at least once, although none became pregnant because unrelated males were absent and daughters avoided incest[d].

References

a Solomon, N.G. and French, J.A. (1997) *Cooperative Breeding in Mammals*, Cambridge University Press

b Mendes Pontes, A.R. and Monteiro da Cruz, M.A.O. (1995) Home range, intergroup transfers, and reproductive status of common marmosets *Callithrix jacchus* in a forest fragment in north-eastern Brazil. *Primates* 36, 335–347

c Abbott, D.H. *et al.* (1998) Adaptations to subordinate status in female marmoset monkeys. *Comp. Biochem. Physiol. C* 119, 261–274

d Saltzman, W. *et al.* (1997) Familial influences on ovulatory function in common marmosets (*Callithrix jacchus*). *Am. J. Primatol.* 41, 159–177

colonies, rank reversals occurred and daughters usurped their mothers. This strongly suggests that a mixture of incest avoidance and dominant control operates in the Damaraland mole-rat, and that, unlike in the naked mole-rat, complete control by the dominant is often not achieved. This is possibly because naked mole-rat queens have often attained their dominant position by fighting with rivals within colonies, whereas in Damaraland mole-rats, breeders often obtain their position by default following the pairing of unrelated individuals.

The evidence for an association between ecological factors, colony dynamics and the proximate control of reproductive skew in African mole-rats seems persuasive. But it remains to be seen whether these observations can be extrapolated more widely to other cooperatively breeding mammals.

Marmosets and mongooses

Clear-cut socially induced physiological blocks to reproductive function can also be seen in female common marmoset monkeys, *Callithrix jacchus*[34] (Box 2), and in female dwarf mongooses, *Helogale parvula*[35]. In both these species nonbreeding males show similar profiles of reproductive hormones to breeders and are not normally observed mating[35,36]. Nonbreeding female dwarf mongooses have lower urinary oestrogen concentrations, which probably compromises induction of ovulation should they mate (dwarf mongooses are thought to be induced ovulators[37]). There can be variation in this suppression within groups, with higher ranking subordinate females having similar endocrine profiles to dominant breeders[35]. As with the naked mole-rat, physiological suppression potentially has an important role to play in maintaining reproductive skew; a study of mongoose in the Serengeti has shown that breeding pairs in a group can commonly be related, and incest is not always avoided. In this population, some 14% of matings were between first order relatives[38]. Socially subordinate female common marmosets are similar to naked mole-rats in that ovarian cyclicity and ovulation is blocked. This phenomenon is especially clear in captive PEER GROUPS of unrelated animals, whereas in family groups, some variation in the degree of physiological suppression of subordinates can be observed (Box 2).

In common marmosets, there is frequent dispersal, resulting in mixed kin social groups. Migration between colonies can be observed in both juvenile and adult males and females, although the bias is reported to be towards females[39]. In the dwarf mongoose, dispersal is weakly male biased and packs are made up of natal individuals and immigrants of both sexes[35]. Therefore, in both marmosets and mongooses, a reproductive conflict of interest might arise in groups, because immigrant individuals unrelated to the breeders of the group will not accrue any inclusive fitness if they remain as nonbreeding helpers (although they might benefit in other ways that are unrelated to kin selection). Conversely, the breeders might gain fitness with the addition of extra helpers, but lose fitness should the immigrants breed. In these mixed-kin groups, control of reproductive skew by incest avoidance alone would obviously fail because of the presence of a number of unrelated mates. In both dwarf mongooses and marmosets, as with naked and Damaraland mole-rats, a high reproductive skew is maintained in most groups by the dominant female (or male) through the physiological suppression of females. Under this scenario, immigrant males would be prevented from breeding as natal females are suppressed, and immigrant females would presumably either usurp the breeding female or become reproductively suppressed by her. Reproductive suppression is known to occur in peer groups of captive common marmosets composed of unrelated adults. Here, nonbreeding females can be reproductively ‘switched on’ by taking them out of social groups where they have subordinate status, thus removing them from the suppressing cues of the dominant. Remarkably, when such females return to subordinate status from being singly housed, or from enjoying dominant status in another group, their reproduction can be ‘switched off’ again[34].

Glossary

Aridity food distribution hypothesis: a theory proposing that the sociality in African mole-rats increases in environments where rainfall is low and unpredictable, and food, in the form of underground roots and tubers is more patchily distributed. As a result, the energetic cost of unsuccessful foraging is greater than in areas of high rainfall.
Cooperative(ly) breeding: A term applied to species that live in social groups, but where reproduction is restricted to certain individuals in the group, and nonbreeders have a helper role, cooperating in the care of offspring other than their own.
Dominant control: One of two models proposed to account for reproductive suppression in females (see also self restraint below). The dominant control model assumes that suppression is maintained by active (usually aggressive) interaction between the dominant breeding female and her subordinate nonbreeders[a].
Eusociality: A specific term that was initially applied to describe social insect societies that fulfil the following criteria: (a) a reproductive division of labour; (b) overlap of generations; and (c) cooperative care of young[b].
Incest and inbreeding: Incest is a term applied to mating among close relatives (parent–offspring or brother–sister). It is at one end of a continuum of mating systems that ranges from fully outbred through more general inbreeding, which includes mating among individuals that share a greater common ancestry than if they had been drawn randomly from the population.
Incest avoidance: An innate response of most sexually reproducing animals that precludes mating with close relatives.
Induced ovulation: A mechanism of ovulatory control whereby the act of mating stimulates ovulation, as opposed to ‘spontaneous’ ovulators, where an endogenous mechanism times the release of eggs.
Peer group: A social group composed of several unrelated adults and offspring from one or more of them (cf. a family group of parents and their offspring).
Philopatry: site fidelity or faithfulness. Natural philopatry refers to animals that remain in, or return to, their place of birth.
Proximate mechanisms: Behavioural and physiological factors that mediate environmental, or ‘ultimate’ factors.
Reproductive skew: An unequal distribution of reproduction among members of a social group, giving rise to ‘breeders’ and ‘nonbreeders’. In a high skew society, reproduction is restricted to one or a small number of individuals of each sex, and nonbreeders have low lifetime reproductive success, or might never breed.
Reproductive suppression: Reproductive skew in societies can be maintained by reproductive suppression of the nonbreeding, socially subordinate group members and mediated by several mechanisms, including one or more of the following: infanticide of the offspring of a subordinate; behavioural exclusion of subordinates from mating opportunities; changes in the physiology of non-breeders that lead to an inhibition of reproduction, such as puberty delay, suppression of ovulation, blocks to implantation; and spontaneous abortion.
Self restraint: A second, alternative model proposed to account for reproductive suppression, where females do not attempt reproduction until an unrelated mate is available for mating[a].

References

a Snowdon, C.T. (1996) Infant care in cooperatively breeding species. *Adv. Stud. Behav.* 25, 643–689
b Wilson, E.O. (1971) *The Insect Societies*, Harvard University Press

Dominant control or incest taboo?

Comparative studies of African mole-rats show that inbreeding avoidance might play an exclusive role in maintaining reproductive skew, particularly in species such as the common mole-rat where natal philopatry is usually short term, and new colony formation by unrelated pairs is usually successful. Where constraints on dispersal are high, colony attrition is low and dominant breeders need to maintain a high degree of reproductive control in groups that might be of mixed relatedness, competitive attempts at reproduction could occur, and ‘self restraint’ is superseded by ‘dominant control’. In the harsh and unpredictable habitats occupied by the Damaraland and naked mole-rats, cooperative behaviour is always needed, and small colonies and pairs tend to be much less successful than are larger established groups, presumably because there are more helpers foraging in these larger groups[14,16].

Studies of other mammalian cooperative breeders are generally congruent with these observations in the African mole-rats. In marmosets and mongooses, nonbreeding helpers are always needed and therefore, because groups might contain a number of unrelated individuals, dominant control of reproduction operates in conjunction with incest avoidance (although in the dwarf mongoose, inbreeding can also occur). Intriguingly, the limited data available suggest that common neuroendocrine and physiological pathways also used to modulate reproduction in other contexts are exploited to mediate these social effects[4]. For example, suppression in both naked mole-rats and common marmosets appears to be similar to sheep, where the seasonally anoestrus ewe is reproductively suppressed by photoperiod. INDUCED OVULATION is also emerging as an important factor to consider in some cooperatively breeding species. This trait could be highly adaptive in situations where mating opportunities are unpredictable, so that ovulations are not wasted when there are no suitable mates available. Thus, in a family group of common mole-rats (which are induced ovulators), nonbreeding females do not waste energy ovulating and their ovaries remain quiescent but ‘primed for action’. As males are not suppressed, mating between dispersing animals, followed by ovulation and conception can potentially be very rapid. Pheromonal control of reproduction could play a similar role in cooperatively breeding microtine rodents such as voles, where urinary chemosignals from unrelated males might be required to ‘activate’ nonbreeding females[40].

The more widespread occurrence of female suppression in cooperatively breeding mammals might also reflect both the increased cost of reproduction in females, compared with males, and the nature of gamete production. Mechanistically, it might be easier to suppress the cyclical production of a comparatively small number of oocytes, compared with the continuous production of millions of spermatozoa (hence the difficulties with developing a human male contraceptive pill). Why then, have naked mole-rats evolved suppression of reproductive physiology in nonbreeding males? This could be explained by the fact that, because of their willingness to inbreed, any male could potentially mate with the queen. Thus, perhaps to maintain social order and reduce aggression, the queen exerts control over these males. Furthermore, control also extends to the consorts of the queen, because testosterone levels in

Acknowledgements
We thank J.U.M. Jarvis, T.M. Burland, S. Le Comber, C. Smith, P. Waser, P. Faulkes and two anonymous referees for discussion and constructive comments on this article; the Foundation for Research Development, South Africa, the Universities of Cape Town and Pretoria, the Zoological Society of London, the Royal Society and the National Geographic Society for financial support; the Wildlife Conservation and Tourism Ministries in Kenya and Namibia; Mr and Mrs H.P. Lühl for permission to work on their farm in Dordabis, Namibia; and the many friends and colleagues who have been involved in both the field and laboratory work connected with our mole-rat studies.

breeding males follow her ovarian cycle, peaking at the time of oestrus and ovulation, when mating occurs.

Fascinating questions remain to be answered, particularly in the void that exists between social cues (behaviour and pheromones) and their neuroendocrine transduction into suppression of reproduction of the individual. This area remains a major empirical challenge. At the population level, microsatellite genotyping is enabling relatedness, reproductive skew and patterns of dispersal to be unambiguously estimated for the first time in many species. In the near future, this information will help to fill in the gap between the theory and the mechanics of how reproductive skew is maintained in cooperative breeders.

References

1 Clutton-Brock, T.H. (1998) Reproductive skew, concessions and limited control. *Trends Ecol. Evol.* 13, 288–292

2 Keller, L. and Reeve, H.K. (1994) Partitioning of reproduction in animal societies. *Trends Ecol. Evol.* 9, 98–102

3 Reeve, H.K. *et al.* (1998) Reproductive sharing in animal societies: reproductive incentives or incomplete control by dominant breeders? *Behav. Ecol.* 9, 267–278

4 Faulkes, C.G. and Abbott, D.H. (1997) Proximate mechanisms regulating a reproductive dictatorship: a single dominant female controls male and female reproduction in colonies of naked mole-rats. In *Cooperative Breeding in Mammals* (Solomon, N.G. and French, J.A., eds), pp. 302–334, Cambridge University Press

5 Pusey, A.E. and Wolf, M. (1996) Inbreeding avoidance in animals. *Trends Ecol. Evol.* 11, 201–206

6 Solomon, N.G. and French, J.A. (1997) *Cooperative Breeding in Mammals*, Cambridge University Press

7 Jarvis, J.U.M. (1981) Eu-sociality in a mammal – cooperative breeding in naked mole-rat *Heterocephalus glaber* colonies. *Science*, 212, 571–573

8 Jarvis, J.U.M. and Bennett, N.C. (1993) Eusociality has evolved independently in two genera of bathyergid mole-rats – but occurs in no other subterranean mammal. *Behav. Ecol. Sociobiol.* 33, 353–360

9 Bennett, N.C. and Faulkes, C.G. (2000) *African Mole-Rats: Ecology and Eusociality*, Cambridge University Press

10 Burda, H. *et al.* (2000) Are naked and common mole-rats eusocial and if so, why? *Behav. Ecol. Sociobiol.* 47, 293–303

11 Lacey, E.A. and Sherman, P.W. (1991) Social organization of naked mole-rat colonies: Evidence for divisions of labor. In *The Biology of the Naked Mole-Rat* (Sherman, P.W. *et al.*, eds), pp. 275–336, Princeton University Press

12 Faulkes, C.G. *et al.* (1991) Hormonal and behavioral aspects of reproduction in female naked mole-rats. In *The Biology of the Naked Mole-Rat* (Sherman, P.W. *et al.*, eds), pp. 426–445, Princeton University Press

13 O'Riain, M.J. *et al.* (1996) A dispersive morph in the naked mole-rat. *Nature* 380, 619–621

14 Braude, S. (2000) dispersal and new colony formation in wild naked mole-rats: evidence against inbreeding as the system of mating. *Behav. Ecol.* 11, 7–12

15 O'Riain, M.J. *et al.* (2000) Morphological castes in a vertebrate. *Proc. Nat. Acad. Sci. U. S. A.* 97, 13194–13197

16 Jarvis, J.U.M. *et al.* (1994) Mammalian eusociality: a family affair. *Trends Ecol. Evol.* 9, 47–51

17 Jarvis, J.U.M. *et al.* (1998) Food availability and foraging by wild colonies of Damaraland mole-rats (*Cryptomys damarensis*): implications for sociality. *Oecologia* 113, 290–298

18 Reeve, H.K. *et al.* (1990) DNA 'fingerprinting' reveals high levels of inbreeding in colonies of the eusocial naked mole-rat. *Proc. Natl. Acad. Sci. U. S. A.* 87, 2496–2500

19 Hamilton, W.D. (1964) The genetical evolution of social behaviour I, II. *J. Theor. Biol.* 7, 1–52

20 Faulkes, C.G. *et al.* (1997) Micro- and macro-geographic genetic structure of colonies of naked mole-rats, *Heterocephalus glaber*. *Mol. Ecol.* 6, 615–628

21 Clarke, F.M. and Faulkes, C.G. (1999) Kin discrimination and female mate choice in the naked mole-rat, *Heterocephalus glaber*. *Proc. R. Soc. London B Biol. Sci.* 266, 1995–2002

22 Cisek, D. (2000) New colony formation in the 'highly inbred' eusocial naked mole-rat: outbreeding is preferred. *Behav. Ecol.* 11, 1–6

23 Bennett, N.C. *et al.* (1996) Reproductive suppression in subordinate, non-breeding female Damaraland mole-rats: two components to a lifetime of socially-induced infertility. *Proc. R. Soc. London B Biol. Sci.* 263, 1599–1603

24 Molteno, A.J. and Bennett, N.C. (2000) Anovulation in non-reproductive female Damaraland mole-rats (*Cryptomys damarensis*). *J. Reprod. Fertil.* 119, 35–41

25 Bennett, N.C. *et al.* (1999) Socially-induced infertility, incest avoidance and the monopoly of reproduction in cooperatively breeding African mole-rats (family Bathyergidae). *Adv. Stud. Behav.* 28, 75–114

26 Maswanganye, K.A. *et al.* (1999) Oligospermia and azoospermia in non-reproductive male Damaraland mole-rats (*Cryptomys damarensis*) (Rodentia: Bathyergidae). *J. Zool. Lond.* 248, 411–418

27 Spinks, A.C. *et al.* (2000) Circulating LH levels and the response to exogenous GnRH in the common mole-rat: implications for reproductive regulation in this social, seasonal breeding species. *Horm. Behav.* 37, 221–228

28 Bennett, N.C. *et al.* (1997) LH responses to single doses of exogenous GnRH by social Mashona mole-rats: a continuum of socially-induced infertility in the family Bathyergidae. *Proc. R. Soc. London B Biol. Sci.* 264, 1001–1006

29 Bennett, N.C. *et al.* (2000) Pituitary sensitivity to exogenous GnRH in giant Zambian mole-rats, *Cryptomys mechowi* (Rodentia: Bathyergidae): support for the socially induced infertility continuum. *J. Zool. Lond.* 252, 447–452

30 Burda, H. (1995) Individual recognition and incest avoidance in eusocial common mole-rats rather than reproductive suppression by parents. *Experientia* 51, 411–413

31 Hazell, R.W.A. *et al.* (2000) Adult dispersal in the cooperatively breeding Damaraland mole-rat, *Cryptomys damarensis*: a case study from the Waterberg region of Namibia. *J. Zool. Lond.* 252, 19–26

32 Spinks, A.C. *et al.* (2000) Differential patterns of philopatry and dispersal in an arid and a mesic population of the common mole-rat, and their implications for the evolution of sociality in the African mole-rats. *J. Anim. Ecol.* 69, 224–234

33 Cooney, R. and Bennett, N.C. (2000) Inbreeding avoidance and reproductive skew in a cooperative mammal. *Proc R. Soc. Lond. B* 267, 801–806

34 Abbott, D.H. *et al.* (1998) Adaptations to subordinate status in female marmoset monkeys. *Comp. Biochem. Physiol. C* 119, 261–274

35 Creel, S.R. and Waser, P.M. (1997) Variation in reproductive suppression among dwarf mongooses: interplay between mechanisms and evolution. In *Cooperative Breeding in Mammals* (Solomon, N.G. and French, J.A., eds), pp. 150–170, Cambridge University Press

36 Baker, J.V. *et al.* (1999) Social determinants of reproductive failure in male common marmosets housed with their natal family. *Anim. Behav.* 58, 501–503

37 Creel, S.R. *et al.* (1992) Behavioural and endocrine mechanisms of reproductive suppression in Serengeti dwarf mongooses. *Anim. Behav.* 43, 231–245

38 Keane B. *et al.* (1996) No evidence of inbreeding avoidance or inbreeding depression in a social carnivore. *Behav. Ecol.* 7, 480–489

39 Mendes Pontes, A.R. and Monteiro da Cruz, M.A.O. (1995) Home range, intergroup transfers, and reproductive status of common marmosets *Callithrix jacchus* in a forest fragment in north-eastern, Brazil. *Primates* 36, 335–347

40 Solomon, N.G. and Getz, L.L. (1997) Examination of alternative hypotheses for cooperative breeding in rodents. In *Cooperative Breeding in Mammals* (Solomon, N.G. and French, J.A., eds), pp. 199–230, Cambridge University Press

41 Willingstorfer, W.J. *et al.* (1998) Ovarian growth and folliculogenesis in breeding and nonbreeding females of a social rodent, the Zambian common mole-rat, *Cryptomys* sp. *J. Morphol.* 237, 33–41

42 Wallace, E.D. and Bennett, N.C. (1998) The colony structure and social organization of the giant Zambian mole-rat, *Cryptomys mechowi*. *J. Zool. Lond.* 244, 51–61

43 Burda, H. (1993) Evolution of eusociality in the Bathyergidae – The case of the giant mole-rats *Cryptomys mechowi*. *Naturwissenschaften* 80, 235–237

44 O'Riain, M.J. *et al.* Reproductive suppression and inbreeding avoidance in wild populations of co-operatively breeding meerkats (*Suricata suricatta*). *Behav. Ecol. Sociobiol.* (in press)

45 Clutton-Brock, T.H. *et al.* (1998) Costs of cooperative behaviour in suricates (*Suricata suricatta*). *Proc. R. Soc. Lond. B* 265, 185–190

46 Clutton-Brock, T.H. *et al.* (2001) Cooperation, control and concession in meerkat groups. *Science* 291, 478–481

47 Smith, D. *et al.* (1997) Is incest common in gray wolf packs? *Behav. Ecol.* 8, 384–391

48 Moelhman, P.D. and Hofer, H. (1997) Cooperative breeding, reproductive suppression, and body mass in canids. In *Cooperative Breeding in Mammals* (Solomon, N.G. and French, J.A., eds), pp. 76–128, Cambridge University Press