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.

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 dominants1 and 'concession' theory involving 'peace' and 'staying' incentives2,3 (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 physiology4. 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 matings5. 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 primates6 (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 insects7,8. Other mole-rats and cooperatively breeding vertebrates might also fit this definition9,10. 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 mass11,12. In addition,
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, fulfill 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’). \(^e\)–\(^d\). Conversely, ‘incomplete control’ models suggest that subordinates breed simply because the dominant is unable to effectively suppress their reproduction, and ‘threat of eviction’ models argue that skew arises from subordinate restraint, to avoid ejection from the social group.

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

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 vertebral in the breeding queen\(^15\).

The 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\(^8\). 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\(^8\), 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, in even naked mole-rats, outbreeding might be the preferred mating system\(^14\),\(^21\).\(^22\),\(^23\).

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
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 inbreeding avoidance alone appears sufficient to maintain reproductive skew within colonies that are essentially family groups. A similar situation can be observed in the Maschona 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.

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

<table>
<thead>
<tr>
<th>Species</th>
<th>No. breeders per group (mean/ max. group sizes)a</th>
<th>Role of helpers</th>
<th>Incest avoidance</th>
<th>Suppression of reproductive physiology in nonbreeders Refs</th>
</tr>
</thead>
<tbody>
<tr>
<td>Naked mole-rats</td>
<td></td>
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<td></td>
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</tr>
<tr>
<td>Heterocephalus glaber</td>
<td>1 female/1–3 males (75/295)</td>
<td>Foraging, defence, pup care</td>
<td>No</td>
<td>Yes</td>
</tr>
<tr>
<td>Cryptomys damarensis</td>
<td>1 female/1–2 males (11/41)</td>
<td>Foraging, defence, pup care</td>
<td>Yes</td>
<td>No</td>
</tr>
<tr>
<td>Cryptomys h. hottentotus</td>
<td>1 female/1 male (5/14)</td>
<td>Foraging</td>
<td>Yes</td>
<td>No</td>
</tr>
<tr>
<td>Cryptomys darlingi</td>
<td>1 female/1 male (7/9)</td>
<td>Foraging</td>
<td>Yes</td>
<td>No</td>
</tr>
<tr>
<td>Cryptomys anselli</td>
<td>1 female/1 male (–20)</td>
<td>Foraging</td>
<td>Yes</td>
<td>No</td>
</tr>
<tr>
<td>Cryptomys mechowi</td>
<td>1 female/1 male (5/11)</td>
<td>Foraging</td>
<td>Yes</td>
<td>No</td>
</tr>
<tr>
<td>Other cooperatively breeding mammals</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Dwarf mongoose (Helogale parvula)</td>
<td>1 female/1 male (mean: 9–15 young)</td>
<td>Antipredator behaviour, care of young</td>
<td>No</td>
<td>No</td>
</tr>
<tr>
<td>Meerkats (Suricata suricatta)</td>
<td>1 female/1 male (range: 2–7)</td>
<td>Antipredator behaviour, care of young</td>
<td>Yes</td>
<td>No</td>
</tr>
<tr>
<td>Common marmosets (Callithrix jacchus)</td>
<td>1 female/1 male (range: 3–15)</td>
<td>Infant carrying</td>
<td>Yes</td>
<td>No</td>
</tr>
<tr>
<td>Gray wolves (Canis lupus)</td>
<td>1 female/1 male (packs number up to 20)</td>
<td>Provision and protect young</td>
<td>Yes</td>
<td>No</td>
</tr>
<tr>
<td>Prairie voles (Microtus ochrogaster)</td>
<td>1 female/1 male (range: 2–19)</td>
<td>Pup care</td>
<td>Yes?</td>
<td>No</td>
</tr>
</tbody>
</table>

aThe data in this column are based on the usual patterns of sociality observed, and deviations are known to occur in most species.
bGroup sizes of up to 60 have been proposed for C. mechowi, but these are based on interviews with local hunters^29 and have not been confirmed by systematic trapping.
cCooperative breeding in these taxa is widespread and has been comprehensively reviewed recently for both canids^48 and rodents^40.

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.
Recent studies attempting to tease apart this enigma are equivocal and demonstrate that control 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. 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

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

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

**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 stable and opportunities for individual reproduction are greater. The Damaraland and mole-rats 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. 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. 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. 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. 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.

References

...show similar profiles of reproductive hormones to breeders and are not normally observed mating.

Nonbreeding female dwarf mongooses have lower urinary oestradiol concentrations, which probably compromises induction of ovulation should they mate (dwarf mongooses are thought to be induced ovulators). There can be variation in this suppression within groups, with higher ranking subordinate females having similar endocrine profiles to dominant breeders. 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. 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, same 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. In the dwarf mongoose, dispersal is weakly male biased and packs are made up of natal individuals and immigrants of both sexes. 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 if 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 off’ 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 on’ again.

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**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.

**Cooperatively 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.

**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.

**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.

**Insect 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 nonbreeders 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.

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**Review**

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breeding males follow her ovarian cycle, peak 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.

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