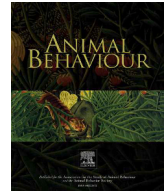






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Subterranean mammalian societies: identity and social architecture in eusocial mole-rats

Daniel W. Hart^{a, *} , Paul J. Jacobs^a, Nigel C. Bennett^{a, b} ^a Department of Zoology and Entomology, University of Pretoria, Hatfield, South Africa^b Mammal Research Institute, Department of Zoology and Entomology, University of Pretoria, Hatfield, South Africa

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Societies are more than groups of animals coexisting; they are structured, enduring communities defined by stable membership, shared identity and relationships that persist across generations. Among mammals, such societies are uncommon but reach their most extreme form in the eusocial African mole-rats, namely the naked mole-rat, *Heterocephalus glaber*, and the Damaraland mole-rat, *Fukomys damarensis*. Eusociality, well known from ants, bees and termites, is a social system loosely comparable to a monarchy, in which a single breeding queen and one or a few males monopolize the colony's reproduction, while other group members suppress their own reproductive potential to serve the needs of the colony. These mole-rats are among the only mammals to fully embody this system, forming long-lived, cooperative colonies with strict boundaries between colony members and outsiders. Yet their strategies for social cohesion diverge. *Fukomys damarensis* depends primarily on individual familiarity to maintain group identity, thereby limiting colony size. In contrast, *H. glaber* uses a shared colony scent and distinct colony-specific vocal dialect to support larger, scalable societies. By comparing these societal extremes, this review explores what makes societies stable, exclusive and resilient, while highlighting the gaps in our current knowledge.

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What sets a society apart from a social group? Societies can be defined as enduring, spatially bounded groups in which individuals exhibit stable membership, shared identity and territoriality (Moffett, 2025). Members consistently distinguish between 'insiders' and 'outsiders', oftentimes responding to the latter with aggression, avoidance or exclusion (Moffett, 2025; Wilson, 2012). Societies, so defined, are characterized by generational continuity, collective control over territory and resources, and mechanisms that reinforce cohesion over time (Moffett, 2025; Olson, 1971). Importantly, membership is not fleeting; it entails a lasting affiliation that shapes social roles, reproductive access and patterns of cooperation (Bowles & Gintis, 2011; Moffett, 2025). Eusocial societies, which fall on the extreme end of the continuum of social complexity (Buffenstein et al., 2022; Nowak et al., 2010) are characterized by highly integrated systems involving reproductive division of labour, cooperative brood care and an overlap in generations in which litters of different ages remain together for their entire lives. They often show high levels of xenophobia, with immigration of outsiders being rare or absent due to the

importance of high relatedness and strict nestmate recognition in maintaining social hierarchy and colony cohesion.

Eusociality is exemplified in mammals by two African mole-rats, the naked mole-rat, *Heterocephalus glaber*, from the arid regions of East Africa, and the Damaraland mole-rat, *Fukomys damarensis*, from the arid and semiarid regions of southern Africa (Bennett & Faulkes, 2000; Jarvis et al., 1994; Lacey & Sherman, 1997; Sherman et al., 1995) (Fig. 1). These subterranean rodents form long-lived colonies that resemble eusocial insect societies in their cohesion, cooperative behaviour, reproductive skew and xenophobia. Colonies typically comprise 10–40 individuals in *F. damarensis* and can exceed 70 individuals in *H. glaber*, although larger groups, up to 300 individuals, commonly stay intact over the long term in captivity (Bennett & Faulkes, 2000). Colonies contain multiple generations of adult offspring, defend exclusive burrow systems and maintain remarkably stable social structures for decades (Bennett & Faulkes, 2000). Crucially, they regulate access to the group and reliably distinguish colony members from outsiders (Bennett & Faulkes, 2000). Yet the means by which identity is encoded, recognized and enforced differs markedly between the two species, reflecting divergent evolutionary solutions to the problem of social cohesion.

* Corresponding author.

E-mail address: daniel.hart@up.ac.za (D. W. Hart).



Figure 1. (a) Naked mole-rats, *Heterocephalus glaber*, colony from Kenya. Photo credit: © Lorna Faulkes. (b) Damaraland mole-rats, *Fukomys damarensis*, colony from Dordabis, Namibia. Photo credit: © Maria Oosthuizen.

Surprisingly, critical information regarding the societal make-up of these only known eusocial mammals remains limited. This review compares how *H. glaber* and *F. damarensis* form, maintain and defend their societies (their unique colonies). We explore how colony identity is constructed and maintained; how territories are delineated and defended; as well as how these closed societies navigate intergroup encounters, including immigration, conflict and the formation of new colonies. These comparisons offer insights into the evolution of mammalian societies, including those elsewhere in the sociality spectrum, such as other social African mole-rats (*Cryptomys* sp.) (Süess et al., 2024).

COLONY FORMATION, MAINTENANCE, GROWTH, STABILITY, EMIGRATION AND IMMIGRATION

Colonies are maintained in both *H. glaber* and *F. damarensis* through monopolized reproduction by a single dominant female (the queen) and one or two males (Bennett et al., 2022). While all offspring are born with full reproductive potential, reproductive roles become rapidly and sharply constrained by social regulation through physiological or behavioural mechanisms induced by the presence of the queen (Bennett & Faulkes, 2000, 2001; Hart, Bennett, & Voigt, 2022; Jarvis, 1981). These nonbreeding colony members of both sexes instead contribute to cooperative activities such as foraging, burrow maintenance and alloparental care (Bennett et al., 2022; Holmes & Goldman, 2021; O’Riain et al., 2000; Siegmann et al., 2021; Thorley et al., 2018), with these nonbreeding colony members forming a dominance hierarchy

associated with size and age. Despite this suppression, in both species some nonbreeding colony members, often referred to as a separate caste labelled ‘dispersal morphs’, can escape reproductive inhibition while still in their natal colony, making them prime candidates for dispersal from their natal colony or for initiating permanent colony division or succession, ultimately founding new colonies (Edwards et al., 2025). Their dispersal morph phenotype is thought to be a set of inherited traits (genetic polymorphism) in these group members, not shared by the remaining nonbreeding colony members that promote individual fitness over colony level cooperation (N. C. Bennett, P. J. Jacobs, & D. W. Hart, personal observations) and is believed to be triggered by seasonal changes in rainfall (Molteno & Bennett, 2002; Young et al., 2010), a change in colony structure (such as increased group size or death of a dominant breeder) and/or individual ageing (Hart et al., 2024). Dispersal morph traits may include accelerated growth, relaxation of reproductive suppression, greater fat reserves and reduced cooperative behaviour (O’Riain et al., 1996; Scantlebury et al., 2006). In dispersal morphs who overcome suppression while still in their natal colony, the release from social inhibition is typically accompanied by morphological and physiological changes, including an increase in reproductive hormones such as testosterone, oestrogen and progesterone (van der Westhuizen et al., 2002; Wallace et al., 2023; Hart et al., 2024; Edwards et al., 2025; N. C. Bennett & D. W. Hart, personal observations).

Dispersal morphs are the predominant colony founders, forming new colonies either through dispersal and independent founding (Braude, 2000; Hazell et al., 2000; Young et al., 2010, 2015) or via permanent colony fission, in which a subset of individuals, led by dispersal morphs, splits away to form a new group separate from the population harbouring the original reproductive individuals or progenitors for the succession of dominant breeders, ensuring the continuity and stability of the social structure (Mynhardt et al., 2021; Sherman et al., 1992). However, the strategies, frequency and modes of new colony formation differ dramatically between species.

In *F. damarensis*, new colonies most often arise when an unrelated dispersal morph male and female pair up after emigrating from separate colonies. Lone dispersal morph females may initially dig a small burrow system, after which they are typically joined by an unrelated dispersal morph male or, in some cases, by a pair of related dispersal morph males (Burland et al., 2002; Jarvis & Bennett, 1993; Thorley et al., 2023). In rare cases, a male dispersal morph enters the tunnel system of a neighbouring colony, copulates with a dispersal morph female and subsequently blocks off sections of the burrow to establish a new colony (N. C. Bennett, personal observations; Bennett et al., 2022). The precise mechanisms by which these individuals locate one another, either while living alone or by coming into contact with a foreign animal while still in their natal colony, remain uncertain, but some individuals may either excavate long exploratory tunnels from their natal colony or inadvertently dig into nearby burrow systems when digging foraging burrows. On rare occasions they may find each other while engaging in random searching above ground (Finn, 2017).

By contrast, the number of dispersal morphs in *H. glaber* colonies is comparatively low, thus resulting in dispersal events being exceedingly rare (Braude, 2000; O’Riain et al., 2000). Although as yet unclear, it may be that those few dispersal morphs seek either to integrate into an established group (see below) or to depart with an unrelated, opposite-sex dispersal morph to initiate a new colony (Faulkes & Bennett, 2013; Faulkes et al., 1997).

Permanent colony fission, especially when space and resource availability allow independent groups to establish, in both species most often follows the death of the queen, or occurs when there is

an increase in colony size that reduces the queen's ability to maintain reproductive suppression over nonbreeders through physical contact, creating social instability (Faulkes & Abbott, 1997; Margulis, Saltzman, & Abbott, 1995). Queen succession through the overthrow of the reigning queen (Clarke & Faulkes, 1997; Medger et al., 2019; D. W. Hart & N. C. Bennett, personal observations) in both species occurs through the elevation of a daughter or, in exceptionally rare cases, replacement by an immigrant dispersal morph female (Mynhardt et al., 2021; Sherman et al., 1992). However, in *F. damarensis*, within-colony queen succession is rare because of strong inbreeding avoidance (Leedale et al., 2024), which is not seen in *H. glaber* (Reeve et al., 1990). When an *F. damarensis* queen dies, succession occurs most commonly through the immigration of an unrelated male taking over the male breeding role, while succession by way of male and female inbreeding within the colony is more common in *H. glaber* (but also see Ciszek, 2000), or through fragmentation of the colony when environmental conditions are ideal (following good rainfall; N. C. Bennett & J. U. M. Jarvis, personal observation). Permanent colony fission typically occurs by subdividing the tunnel system through the backfilling of connecting passageways, reducing contact and potential conflict between the emergent colonies. The resultant colonies are frequently unequal in size. The smaller units are often forced to settle in resource-poor areas where they rarely persist beyond their first litter if subsequent rainfall is scarce, likely because they are unable to excavate sufficiently extensive burrow systems to access adequate food resources (N. C. Bennett & J. U. M. Jarvis, personal observations).

The majority of individuals remain within their natal colonies as nonbreeding colony members (over 99% in *H. glaber* and approximately 70% in *F. damarensis*; Bennett & Faulkes, 2000; Brett, 1991; P. J. Jacobs et al., 2021; Sherman et al., 1995). The higher retention of nonbreeding colony members in *H. glaber* likely reflects a combination of the greater tolerance for inbreeding in this species and the high risks associated with solitary living in their extremely arid habitats (Hart, Bennett, Oosthuizen, et al., 2022).

Once established and reproducing successfully, colonies of both species exhibit remarkable longevity and stability, persisting for more than 18 years in captivity and typically 6–10 years in the wild (Buffenstein & Amoroso, 2024; N. C. Bennett, personal observations).

The permanent integration of unrelated individuals is rare, as unfamiliar individuals are typically met with intense aggression (D. S. Jacobs et al., 1998; O'Riain & Jarvis, 1997). Evidence for *F. damarensis* suggests that slow, progressive exposure to unfamiliar individuals can reduce the frequency of attacks on the immigrant, eventually allowing integration; however, this relies on the opportunity for social spacing that permits interactions to occur gradually (Kelley et al., 2019).

In *H. glaber*, integration of outside adult animals is largely restricted to dispersal morphs or young nonbreeding colony members (most often pups), and even then, occurs only rarely. However, evidence for the incorporation of foreign pups that were fostered after an intercolony invasion is growing (Braude et al., 2021; also see below).

Although mole-rats are generally xenophobic, once immigrants or foreign pups are integrated into a colony, they appear to be treated similarly to natal individuals, with no clear evidence of discrimination.

RECOGNITION AND SOCIETAL IDENTITY

The cohesion of a society relies on mechanisms that allow individuals to distinguish 'insiders' from 'outsiders'. These

recognition processes underpin cooperation, reproductive regulation and collective defence. In eusocial mole-rats, identification arises from learned or emergent cues that encode group membership, oftentimes coincident with kinship.

In *F. damarensis*, social recognition is grounded in direct familiarity (Caspar et al., 2022; Leedale et al., 2021; Nichols et al., 2025). Individuals learn the odours and behavioural profiles of each colony-mate through repeated interactions (Cooney, 2002; Cooney & Bennett, 2000; D. S. Jacobs & Kuiper, 2000; Kelley et al., 2019; Leedale et al., 2024). As such, social cohesion relies on prior exposure: unfamiliar individuals, even close kin, are typically treated as intruders, whereas familiar, but unrelated, individuals may be tolerated.

In contrast, *H. glaber* exhibits colony level recognition mediated by a shared olfactory signature (Clarke & Faulkes, 1999; Judd, 1996; O'Riain & Jarvis, 1997; Toor et al., 2015; but also see Faulkes & Abbott, 1993; Smith et al., 1997) and vocal dialect (Barker et al., 2021). Colony-specific odours in *H. glaber*, apparently lacking in *F. damarensis* (Nichols et al., 2025), appear to be an emergent property derived from shared microbial communities, metabolic products and possibly dietary homogeneity, gained through frequent body contact. This 'societal scent' enables recognition at a scale far exceeding individual familiarity, supporting stable colonies of over 300 members in captivity. In other mammals, like certain cetaceans and humans, that form large social groups, shared vocal dialects (or 'accents') in *H. glaber* play a comparable role in reinforcing group identity. However, colony dialect is flexible and dictated by the queen, with a dialect shift occurring after queen succession (Barker et al., 2021). Such vocal changes are learnable, particularly by younger individuals, facilitating their continued acceptance within the colony (Barker et al., 2021). Notably, *H. glaber* colonies have been observed to raid neighbours and abduct pups and successfully incorporate these pups into their own workforce. This implies that identification with the society is established and learned at a young age, with neighbouring colonies perhaps sharing sufficiently similar microbial/diet-derived scent profiles to simplify olfactory assimilation. As with immature ants, because unweaned pups lack a fully developed colony-specific signature (scent or vocal dialect), they may be more easily assimilated into a new societal identity, facilitating cross-boundary recruitment (Braude et al., 2021). While tactile cues (Schwark et al., 2024) also play a role in social interactions, olfaction and vocalization are thought to be the dominant, if not the sole, modality for identity recognition. *Fukomys damarensis* also has a fairly large repertoire of vocalizations, but no colony-specific dialects or signature greetings have been documented to date.

While very little research has focused on disperser morphs, it is possible that these individuals possess traits that increase their chances of acceptance by colonies, for instance, in *H. glaber* through individual odour variation or differences in vocal dialect, however, this remains speculative.

TERRITORIALITY AND INTERGROUP CONFLICT

A defining feature of societies is their control of separate spaces. Both *F. damarensis* and *H. glaber* establish and protect discrete burrow systems. The colonies of both species remain spatially separate, and boundaries between groups appear stable over time (N. C. Bennett, personal observations; Finn, 2017). Yet their territorial strategies diverge in ways that reflect fundamental differences in social cohesion and group identity (Braude et al., 2021; Cooney & Bennett, 2000).

In *F. damarensis*, territorial defence is usually the responsibility of the breeding pair when colonies come into contact, typically by

chance during tunnel expansion and foraging. Nonbreeding colony members rarely participate in aggression, likely because their indirect fitness is less affected by colony expansion or defence (Carter et al., 2014; Cooney, 2002). Intruders are repelled with aggression, and there is little evidence of cooperative territorial expansion (Cooney, 2002; Cooney & Bennett, 2000).

In contrast, *H. glaber* exhibits more collective and dynamic territorial behaviour. All nonbreeding colony members actively participate in group defence, and on very rare occasions, entire colonies may mount offensive expansions by invading neighbouring burrow systems and abducting pups in a striking parallel with slave-raiding ants (Braude et al., 2021). These conflicts usually occur when expanding tunnel systems intersect rather than through targeted scouting, and once contact is made, intense physical battles may ensue. Colonies fight as cohesive units, with the largest individuals (sometimes called soldiers) taking the lead (Toor et al., 2022) while the breeders tend to retreat (D. W. Hart, personal observations). Combat involves biting and grappling, sometimes resulting in injury or death, particularly among the soldiers, and outcomes are strongly shaped by relative colony size: larger groups can overwhelm and displace smaller ones, sometimes seizing their tunnel systems wholesale. Such behaviour suggests that territory is not merely defended but actively deployed as a vector for growth and dominance (Braude et al., 2021).

Environmental conditions modulate territorial dynamics in both species. Rainfall and softened soils can enable the expansion of tunnel systems, and hence areas under territorial control, while durable tunnels may promote spatial persistence (Finn, 2017). In *F. damarensis*, low population density environments may support the gradual expansion and eventual division of larger colonies (Finn, 2017). Behaviours such as ‘pumping’ (a wave-like motion performed by animals to increase air and scent circulation in the tunnel systems) (Burda, 2022; Eloff, 1958) and tunnel plugging (Majelantle et al., 2022, 2024) have been proposed to contribute to territory defence or maintenance, but their precise functions remain unresolved. Much remains unknown for both species: how spatial boundaries shift over time, whether some tunnel systems carry special status (e.g. inherited or preferentially defended) and how landscape structure shapes patterns of conflict and coexistence (Braude et al., 2021).

SOCIETIES IN THE SUBTERRANEAN SPECTRUM

As eusocial species, *F. damarensis* and *H. glaber* represent an extreme end point along a continuum of mammalian social complexity. Both species exemplify what defines a society: a long-lived, territorially bound group characterized by stable membership, internal cohesion and a shared sense of identity. These are not merely aggregations of individuals, but structured collectives in which members recognize one another as belonging to the group and behave accordingly over time. Group membership represents a persistent social identity that can endure across the generations of broods from subsequent queens, influencing both cooperative behaviours within the colony and competitive interactions with other groups.

Despite these shared societal features, *F. damarensis* and *H. glaber* reach these identities through divergent pathways. *Heterocephalus glaber* illustrates how emergent colony level identity, through a shared identity cue (an odour and vocal dialect), can facilitate the scaling of societies: although rare, the assimilation of outsiders, possibly involving pup kidnapping/fostering, demonstrates a capacity for flexibility in *H. glaber*. Social behaviours in this species are tightly synchronized, underpinned by stable, colony-specific cues that enable both the integration and the

selective rejection of intruders. By contrast, *F. damarensis* societies are maintained through a more conservative mechanism: cohesion emerges from shared history and social familiarity between individuals, which, nevertheless likewise allows for pup fostering and reproductive roles that are strictly regulated.

Together, *F. damarensis* and *H. glaber* offer a powerful comparative model for uncovering the different ways by which mammalian societies can manage identity, cohesion and membership. Their social complexity exposes key questions that cut to the heart of social evolution. What sensory, chemical or behavioural cues govern recognition and the exclusion of outsiders? Can assimilated individuals achieve full integration across all developmental stages? Do colony-specific scent profiles shift with age, diet or demography? And how are intergroup boundaries established, maintained or breached in different ecological contexts?

Answering these questions will shed light on the proximate mechanisms and evolutionary forces that shape stable, highly complex societies. These eusocial species demonstrate that sociality alone does not make a society. It is the persistent regulation of group identity, through history, recognition, exclusion, and sometimes assimilation, that defines the societal condition, here in its most refined, subterranean form.

Author Contributions

Daniel W. Hart: Writing – original draft, Project administration, Conceptualization. **Paul J. Jacobs:** Writing – original draft, Project administration, Conceptualization. **Nigel C. Bennett:** Writing – original draft, Project administration, Conceptualization.

Data Availability

No data were used for the research described in the article.

Declaration of Interest

The authors declare that they have no conflicts of interest.

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