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No task specialization among helpers in Damaraland mole-rats

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The specialization of individuals in specific behavioural tasks is often attributed either to irreversible differences in development, which generate functionally divergent cooperative phenotypes, or to age-related changes in the relative frequency with which individuals perform different cooperative activities; both of which are common in many insect caste systems. However, contrasts in cooperative behaviour can take other forms and, to date, few studies of cooperative behaviour in vertebrates have explored the effects of age, adult phenotype and early development on individual differences in cooperative behaviour in sufficient detail to discriminate between these alternatives. Here, we used multinomial models to quantify the extent of behavioural specialization within nonreproductive Damaraland mole-rats, *Fukomys damarensis*, at different ages. We showed that, although there were large differences between individuals in their contribution to cooperative activities, there was no evidence of individual specialization in cooperative activities that resembled the differences found in insect societies with distinct castes where individual contributions to different activities are negatively related to each other. Instead, individual differences in helping behaviour appeared to be the result of age-related changes in the extent to which individuals committed to all forms of helping. A similar pattern is observed in cooperatively breeding meerkats, *Suricata suricatta*, and there is no unequivocal evidence of caste differentiation in any cooperative vertebrate. The multinomial models we employed offer a powerful heuristic tool to explore task specialization and developmental divergence across social taxa and provide an analytical approach that may be useful in exploring the distribution of different forms of helping behaviour in other cooperative species.

The morphological and behavioural specialization of individuals to specific tasks is a common feature of complex insect societies (Maynard Smith & Szathmáry, 1995; Wilson, 1971). To infer specialization it is necessary to show that investment in one cooperative behaviour trades off against investment other forms of cooperative behaviour. In this context, species differ in the extent to which individuals become irreversibly committed to specific roles (Beekman, Peeters, & O'Riain, 2006; English, Browning, & Raihani, 2015), and the extent to which they do so is commonly regarded as an indicator of the complexity of their society on the basis that increased division of labour improves efficiency (Bourke, 1999; Oster & Wilson, 1978; but see Dornhaus, 2008). Some of the most extreme examples are provided by species of eusocial insect where discrete and permanent phenotypic differences exist between functionally sterile workers that focus on different tasks, such as brood care, colony defence or foraging (Bourke & Franks, 1995; Hölldobler & Wilson, 1990; Michener, 1969; Roisin & Korb, 2010). In contrast, in some other social insects, specialization is more labile, and trade-offs are apparent in the form of temporal castes where task allocation varies with age as nonreproductive individuals shift from one role to another; as in honeybees, *Apis mellifera* (Seeley, 1982), some lower termites (Korb & Hartfelder, 2008; Noirot & Pasteels, 1987) and fungus-cultivating ambrosia

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beetles (Biedermann & Taborsky, 2011). Evidence of behavioural specialization is rare outside of the social insects, but studies of some cooperative mammals have argued that in some species that breed cooperatively, nonreproductive helpers display forms of task specialization analogous to those of castes in social insects.

The case for behavioural specialization in cooperatively breeding mammals has been most strongly advanced for several of the social African mole-rats, including the naked mole-rat, *Heterocephalus glaber*, and the Damaraland mole-rat, *Fukomys damarensis*. In these two species it has been suggested that individuals can be separated into discrete functional groups that differ in their relative contributions to different cooperative activities (Bennett & Faulkes, 2000; Bennett & Jarvis, 1988; Jarvis, 1981; Scantlebury, Speakman, Oosthuizen, Roper, & Bennett, 2006) and their probability of dispersing (O'Riain, Jarvis, & Faulkes, 1996), as well as in related aspects of their size and shape (Bennett & Faulkes, 2000). However, other studies of the distribution of cooperative behaviour in social mole-rats found continuous rather than discrete differences between individuals in their cooperative contributions (Lacey & Sherman, 1991), and a recent study in Damaraland mole-rats has suggested that helpers do not specialize in specific tasks but rather vary in overall helpfulness (Zöttl, Vullioud, et al., 2016).

Determining whether individuals within cooperative societies are behaviourally specialized is more complex than initially appears as the expression of cooperative behaviour can vary between and within individuals in many ways. For example, individuals may differ either in their general contribution to all cooperative activities or in their relative contributions to specific activities. In addition, relative differences in behaviour may be (1) largely driven by age, (2) unrelated to either age or adult phenotype, or (3) associated with contrasts in both adult phenotype and early development, as in the caste systems of many eusocial insects (see Table 1). There may also be many different combinations and subdivisions of the four distributions of cooperative behaviour shown in Table 1. Without longitudinal studies of the behaviour of individuals at different ages, it is often impossible to distinguish between the developmental processes leading to individual differences in behaviour or to allocate societies to different categories. With this information, it is possible to examine the extent to which cooperative behaviours are correlated within individuals, the temporal stability of any correlations across development, and other phenotypic determinants of behaviour, which together underpin the distribution of behaviour across individuals in cooperative societies.

Although earlier studies of social mole-rats have described contrasts in cooperative behaviour between individuals and suggested that they are a consequence of variation in development (Bennett & Jarvis, 1988; Burda, 1990; Lacey & Sherman, 1991), the absence of longitudinal data for individuals has made it impossible to tell whether or not individual differences are a consequence of permanent contrasts in development analogous to those found in insect societies with distinct castes. More recently, Mooney, Filice, Douglas, and Holmes (2015) used a combination of in-group observations and out-of-group tests of pup care and colony defence in naked mole-rats and showed that contributions to different cooperative tasks (work-related tasks, pup care and colony defence) varied across nonbreeding group members in naked mole-rats, and that the expression of these behaviours was stable across time and across litters. They also showed that there was a trade-off between pup care and both colony defence and working behaviour that is suggestive of task specialization. In contrast, recent research on Damaraland mole-rats has shown that individual differences in contributions to cooperative effort are a consequence partly of differences in age and growth and partly of variation in

Table 1
Forms of individual variation in cooperative behaviour across cooperative societies

Description of variation in cooperative behaviour across individuals	Trade-offs	Early development	Age	Adult phenotype[p]	Examples
Differences in all forms of cooperative behaviour associated with age; temporary and permanent specialization absent	✗	✗	✓	✗	Meerkat, *Suricata suricatta*[a] White-winged chough, *Corcorax melanorhamphos*[b] Social spider, *Anelosimus eximius*[c] Damaraland mole-rat, *Fukomys damarensis*[d]
Specialization in cooperative behaviour independent of age or adult phenotype	✓	✗	✗	✗	Social spider, *Anelosimus studiosus*[e] Lion, *Panthera leo*[f] Chimpanzee, *Pan troglodytes*[g]
Specialization in cooperative behaviour associated with age	✓	✗	✓	✗	Princess of Burundi cichlid, *Neolamprologus pulcher*[h] Honeybee, *Apis mellifera*[i] Paper wasp, *Polistes canadensis*[j] Ambrosia beetle, *Xyleborinus saxenseni*[k]
Specialization in cooperative behaviour associated with contrasts in both adult phenotype and early development	✓	✓	✗	✓	Leafcutter ant, *Acromyrmex echinatior*[l] Big-headed ant, *Pheidole megacephala*[m] Nasute termite, *Velocitermes barrocoloradensis*[n] Aphid, *Tuberaphis styraci*[o]

[a] Clutton-Brock et al. (2003).
[b] Heinsohn and Cockburn (1994).
[c] Settepani, Grinsted, Granfeldt, Jensen, and Bilde (2013).
[d] Zöttl et al. (2016), this study.
[e] Wright et al. (2014).
[f] Stander (1992).
[g] Boesch (2002).
[h] Bruintjes and Taborsky (2011).
[i] Seeley (1982).
[j] Giray, Giovanetti, and West-Eberhard (2005).
[k] Biedermann and Taborsky (2011).
[l] Hughes, Sumner, Van Borm, and Boomsma (2003).
[m] Sameshima, Miura, and Matsumoto (2004).
[n] Roisin (1996).
[o] Shibao, Kutsukake, Matsuyama, Fukatsu, and Shimada (2010).
[p] Qualitative nonbehavioural differences in adult phenotype.