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Task specialization and task switching in eusocial mammals

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Eusocial insects often display a certain degree of task specialization, which may help maximize the efficiency of a colony. Here we tested for the presence of task specialization in a eusocial mammal. Naked mole-rats, *Heterocephalus glaber*, were videorecorded across multiple days in their home colony and in a neutral arena with an unfamiliar conspecific for determination of short-term behavioural profiles. They were also recorded in these settings across the birth of multiple litters to assess the stability of behaviour patterns over months. Pup care behaviour, working behaviour and colony defence were unevenly distributed among subordinate mole-rats. Furthermore, these behaviours were stable across days and months. Across days, age was positively related to colony defence and negatively related to pup carrying. We also tested whether behaviours were stable across contexts by observing pup care behaviour outside of the colony in a neutral arena. We further attempted to determine whether mole-rats' behaviours were contingent on the demands of the colony by removing the most frequent performers of pup care, colony defence and work behaviour from each colony. Results from these experiments suggest that when task specialists were no longer present, remaining animals adjusted their behaviour to fill the needs of the colony. Under these circumstances, younger animals engaged in the majority of working and pup-carrying behaviour while older animals engaged in the majority of colony defence behaviours. Thus, subordinate naked mole-rats show both task specialization and task switching.

In large social groups where a diverse array of behaviours are required, task specialization may help to avoid superfluous labour and can promote group efficiency when the roles exhibited meet current societal needs. This specialization may contribute to the success of social insects (Jeanne, 1986; Wilson, 1987) and has been demonstrated in a number of eusocial species (e.g. honeybees: Free, 1964; eusocial wasps: Jeanne, 1986; termites: Noirot, 1989; ants: Wilson, 1976). More recently, researchers have begun to uncover the molecular mechanisms underlying this specialization (reviewed in: Feldmeyer, Elsner, & Foitzik, 2014; Lattorff and Moritz, 2013), although many of these may be species specific (Manfredini et al., 2014). Importantly, eusocial insects may switch roles based on internal factors such as the ratio of workers in certain roles (Wilson, 1984), external factors imposed on the colony from the environment (Gordon, 1989) or, more likely, a combination of both. Thus, while task specialization may increase the economy of a society, the potential for task switching helps to meet changing societal demands.

The coordinated efforts that make insect societies so successful appear to have analogues in noneusocial mammalian social groups. For example, mound-building mice, *Mus spicilegus*, construct collective underground nests in which they spend the winter. While over 10 animals may ultimately inhabit this nest (Muntyanu, 1990), only a select few within the group build it. When conditions for nest building were mimicked in the laboratory, two of six mice per group reliably accounted for almost 80% of the nest building, and this task specialization was consistent across days (Serra et al., 2012). Similar task specialization may be seen in hunting behaviour in large mammals such as lions, *Panthera leo* (Stander, 1992) and bottlenose dolphins, *Tursiops truncatus* (Gazda, Connor, Edgar, & Cox, 2005).

The naked mole-rat, *Heterocephalus glaber*, is rare among mammals in that, not only is it one of few mammalian species that are designated as eusocial, but its reproductive skew far surpasses others in that category. Naked mole-rat colonies can contain hundreds of animals, yet they contain only one breeding female and one to three breeding males (Brett, 1991a, 1991b; Jarvis, 1981). The remainder of the animals are nonreproductive subordinates that

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fulfil the labour-related tasks of the colony such as colony maintenance/construction, alloparental pup care and colony defence (Jarvis, 1981; Lacey & Sherman, 1991).

Because naked mole-rat colonies are large, they face ecological pressures from food scarcity and costs of subterranean living (Brett, 1991a, 1991b); thus, task specialization could serve to maximize the economics of physical exertion among colony members. Jarvis (1981) first proposed that subordinates do not all work at the same rate, using the terminology of frequent workers, infrequent workers and nonworkers. She suggested that these animals show a version of polyethism, where the roles of individuals are based on their relative body mass in the colony rather than their absolute age (with heavier animals generally, but not always, being older). However, these relationships were not consistently demonstrated. Lacey and Sherman (1991) and Jarvis, O'Riain, and McDaid (1991) found conflicting results when attempting to correlate body mass with digging behaviour. Furthermore, this characterization was based solely on labour-related tasks such as digging and foraging. Naked mole-rat subordinates fulfil other roles in the colony such as alloparental care and defence against intruders. Lacey and Sherman (1991) extended the findings of Jarvis to show that smaller animals tend to engage in pushing pups (pup care) and colony maintenance more often, while heavier animals tend to perform colony defence behaviours at a higher rate. In all cases, division of labour is based on the hypothesis that working behaviours vary with the size, body mass or age of the individual. While temporal stability of these behavioural traits was suggested (Lacey & Sherman, 1991), it has yet to be directly measured in naked mole-rats. Although Bennett (1990) showed that a very similar division of labour in the Damaraland mole-rat, *Cryptomys damarensis*, is maintained over a 2-year period and that frequency of working behaviour is related to a number of social behaviours in the colony. Characterizing naked mole-rats based on their frequency of a number of behaviours may, therefore, yield interesting results of complete behavioural profiles of animals.

Here we tested whether subordinate naked mole-rats show task specialization, asking whether their performance of one behaviour is related to their performance of other behaviours and/or to the physical characteristics of the animal. We also tested whether any specialization is stable both in the short (days) or long (months) term. In experiment 1, we recorded behaviour and demographics of animals within each colony and during exposure to unfamiliar conspecifics, using factor analysis to determine whether behaviours clustered in a meaningful way. We also correlated behaviours across multiple testing days to determine the stability of behavioural traits. In experiment 2, we recorded the behaviour of animals within each colony and their interaction with unfamiliar animals across the birth of multiple litters to see whether behavioural traits were stable for a longer period. We also measured alloparental care outside of the colony to see whether in-colony behaviours were stable across contexts. While differences in growth rates may prepare certain animals for filling various roles in the colony (Jarvis, 1981), it is unclear whether subordinates switch tasks based on changing demands of the colony. To test this, we removed subordinates that performed high levels of certain behaviours relative to their colony-mates to see whether this affected task specialization in the remaining animals.

METHODS

Experiment 1: Short-term Task Specialization

Animals and behavioural tests

Adult subordinate naked mole-rats from captive colonies were used. Colony founders descended from animals obtained from Dr Bruce Goldman at the University of Connecticut (for additional history see Peroulakis, Goldman, & Forger, 2002). Naked mole-rat colonies were housed at the University of Toronto Mississauga vivarium in large ($45.75 \times 24 \times 15.25$ cm high) and small ($30 \times 18 \times 13$ cm high) polycarbonate cages connected by plastic tubes (25 cm long, 5 cm in diameter). Rooms were kept on a 12:12 h light/dark cycle at 28–30 °C. Animals had ad libitum access to a diet of sweet potato and wet 19% protein mash (Harlan Laboratories, Inc.). We marked 48 animals from three colonies (colonies A, B and C; 16 from each colony) on their backs with distinct colours and symbols for identification. We then videorecorded each colony with Sony Handycams® on 3 days for 30 min each day (with 48 h between recording days). We scored these videos using the ObserverXT event recording software (Noldus Information Technology, Wageningen, The Netherlands). In-colony behaviours of interest were the duration of work behaviours (digging and colony maintenance) and the duration of pup care behaviour (carrying pups). In addition, the same animals were used for paired interaction tests. Each animal was individually placed in a polycarbonate cage ($43 \times 22 \times 21$ cm high) with an unfamiliar stimulus animal from another colony. Stimulus animals were pre-screened to ensure that they were not initiators of aggressive behaviours towards unfamiliar animals. The pairs were then recorded for 10 min. This was repeated twice over 2 days with 48 h between each test (during the 2-day interval between colony testing). Each individual animal was exposed to a different stimulus animal at each time point and stimulus animals were varied between tests to avoid habituation to the stimulus. These videos were scored for duration of aggression towards and interest in (investigation of) the unfamiliar stimulus mole-rat. No injuries requiring veterinary attention were inflicted on either target or stimulus animals. All procedures adhered to federal and institutional guidelines and were approved by the University Animal Care Committee (animal use protocol numbers 20009986 and 20009987).

Body fat percentage

After behavioural testing was complete, we screened experimental animals for body fat percentage. We measured total fat mass using dual energy–X-ray absorptiometry (DXA; Hologic QDR4500; Hologic, Inc., Waltham, MA, U.S.A.) under light anaesthesia (isoflurane inhalation). Measurements of fat body mass (FBM), total mass and FBM% were obtained for each scan using rat whole-body software (Hologic QDR software, v.12.3). Following recovery from anaesthesia, animals were immediately returned to their colony. No negative effects of anaesthesia or temporary colony separation were detected.

Statistical analyses

One goal of the study was to determine whether different behaviours grouped together in a reliable way. There have been attempts to relate various behaviours to body mass or age along with some suggestions and some disagreements about whether these variables are important for predicting which behaviours an animal might show (Jarvis, 1981; Jarvis et al., 1991; Lacey & Sherman, 1991; O'Riain & Jarvis, 1997). We therefore used factor analysis to try to understand whether various factors might underlie variations in behavioural and demographic variables. To accomplish this, we used principal axis factoring on SPSS v.17 (SPSS Inc., Chicago, IL, U.S.A.). Included variables were FBM%, age (in months), in-colony working behaviour, in-colony pup care, and interest in and aggression towards unfamiliar conspecifics. We then averaged these scores across testing days for each animal. FBM% was chosen as a variable in the factor analysis over total body mass as it was more closely associated with some of the behaviour variables (Supplementary Table S1). To account for the sex and colony of