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EDITORIAL

Workers require more cognitive skills than soldiers, queens and kings

M. Beekman[1]

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We all know that human kings and queens do not obtain their status due to their intellect, at least not in hereditary monarchies. To prove the point, one king, King George III of Great Britain and Ireland, was decidedly mad, so mad that he is known in children's history books as the "mad king who lost America." The American colonies were lost during his reign (1801–1820), but their loss probably had more to do with the political times than with his madness.

Living in a society does place cognitive demands on the individuals within it, but human kings and queens can do without high levels of cognitive skill because of the many minions that surround them. In species that are facultatively social, increased competition associated with the formation of aggregations can result in modifications to the brain to accommodate changes in social structure. Desert locusts are probably the best example. During their transition from a solitary life to forming massive aggregations, competition for salt and protein results in large-scale cannibalism (Simpson et al. 2006). The change from a quiet life, just living by oneself, to one in which one is surrounded by thousands of others, is associated with an increase in brain investment and greater relative investment in the mushroom bodies, the cognitive integration regions of the insect brain (Ott and Rogers 2010). Changes to brain investment with increased levels of sociality are even found in species that are not normally social but are artificially forced to become so. *Drosophila melanogaster* fruit flies invest more in neural development when crowded as larvae (Heisenberg et al. 1995) probably so that the resulting adults are better able to cope with competition.

The idea that increased levels of sociality lead to an increase in neural investment became known as the 'social brain hypothesis' (Dunbar 1998). The larger the group, the greater the cognitive demands are until cognitive abilities limit a further increase in group size. The social brain hypothesis has found support not only in mammals, primates in particular, but also in some social insects. Comparing the volumes of the mushroom body calyces of two closely related species of bees, one that has lost social behaviour, the other social, Pahlke et al. (2020) found that the loss of sociality was associated with a loss in relative neural investment in the mushroom body calyces.

Support for the social brain hypothesis in social insects should not come as a surprise to those who know that while best known from the primate literature, the hypothesis has its real origin in the social insects (Lihoreau et al. 2012). In 1850, Durjardin noticed how the mushroom bodies of honeybees were significantly enlarged and proposed that these brain areas were the seat of insect 'intelligence'. Since then, a relationship between the size of the mushroom body, advanced cognition, and sociality is often implied (Lihoreau et al. 2012) but less often tested explicitly. One could also argue the complete opposite to the social brain hypothesis. Many of the behavioural innovations found in the social insects in fact require *less* cognitive skills compared with their solitary counterparts (Lihoreau et al. 2012). Particularly in species with distinct behavioural and reproductive castes, specialising in a particular task could lead to a *reduction* in cognitive skills. Which finally takes me back to kings and queens, but this time of the termite version of royalty.

In this issue, O'Donnell et al. (2022) take a neuroecological approach to investigate if the sizes of two key brain neuropils, the antennal lobes, which are the centres of chemosensory integration, and the mushroom bodies, differ amongst the different castes of *Zootermopsis* termites. Workers in many social insects perform a variety of tasks and it could be argued that workers, therefore, require more cognitive skills compared with reproductives. On the other hand, becoming the reproductively dominant individual, and then maintaining that position, also requires cognitive skills. It is thus not surprising that studies have found both a positive and a negative association between caste and relative brain region depending on the species.

✉ M. Beekman
madeleine.beekman@sydney.edu.au

[1] Behaviour, Ecology and Evolution (BEE) Lab, School of Life and Environmental Sciences, The University of Sydney, Camperdown, Australia

Disentangling the role of caste on relative brain size is made even more complicated in species with irreversible caste differentiation, where those who become workers and those who become reproductives are different from the moment they hatch from the egg. Dampwood termites from the genus *Zootermopsis* are ideal to test the relationship between caste, or more precisely tasks performed, and brain development. Nymphs remain developmentally plastic for a large part of their life during which time they perform the colony's main worker functions. As they mature, they can differentiate into specialist defenders (soldiers) or reproductives (kings and queens).

O'Donnell et al. (2022) tested the following hypotheses: (1) reproduction demands greater brain investment, in which case the kings and queens would have relatively greater brain tissue investment than their sterile helpers, or (2) performing worker tasks requires greater brain investment, resulting in the workers having greater brain investment compared with kings and queens (no differences were expected between the sexes, a prediction that was confirmed). An interesting twist on *Zootermopsis* castes is that soldiers can also become replacement reproductives, allowing an independent test for cognitive demands of reproduction.

Zootermopsis termite soldiers, and kings and queens, had significantly reduced relative investment in antennal lobes and mushroom bodies, strongly suggesting that reproduction is cognitively less demanding than working. Reproductive soldier brains were similar to typical soldier brains, further arguing against a cognitive boost for reproductives.

O'Donnell et al's (2022) results nicely illustrate how the brain adapts developmentally to the challenges the individual is faced with. Such brain plasticity also explains why different studies on different species do not necessarily find the same association between caste and brain investment. Biology would not be so interesting if the details of the species did not matter.

References

Dunbar RIM (1998) The social brain hypothesis. Evolut Anthropol Issues News Rev 6:178–190

Heisenberg M, Heusipp M, Wanke C (1995) Structural plasticity in the *Drosophil*a brain. J Neurosci 15:1951–1960

Lihoreau M, Latty T, Chittka L (2012) An exploration of the social brain hypothesis in insects. Front Physiol 3:442. https://doi.org/10.3389/fphys.2012.00442

O'Donnell S, Bulova SJ, Barrett M (2022) Brain plasticity indicates key cognitive demands in an animal society: caste comparisons in dampwood termites. Insectes Sociaux

Ott SR, Rogers SM (2010) Gregarious desert locusts have substantially larger brains with altered proportions compared with the solitarious phase. Proc R Soc B Biol Sci 277:3087–3096

Pahlke S, Seid MA, Jaumann S, Smith A (2020) The loss of sociality is accompanied by reduced neural investment in mushroom body volume in the sweat bee *Augochlora pura* (Hymenoptera: Halictidae). Ann Entomol Soc Am 114:637–642

Simpson SJ, Sword GA, Lorch PD, Couzin ID (2006) Cannibal crickets on a forced march for protein and salt. Proc Natl Acad Sci 103:4152–4156