Commentary

Who is the Queen's mother? Royal cheats in social insects

Ant and bee colonies have often served as allegorical models for ideal human societies (Ridley 1996). This view is nicely illustrated by Shakespeare's *King Henry V* (act 1, scene 2) in which a bee colony is depicted as a benevolent dictatorship with the workers carrying out complementary tasks and living in harmonious obedience to a caring monarch, much like Elizabethan England should have been. It is amusing that despite a Queen being in control in England, Shakespeare assumed that the social insects were governed by a King. Shakespeare built his play around the fact that human societies are full of conflict and cheaters, whereas in insect societies there are none. Or are there?

A recent paper by Hughes and Boomsma (2008) has identified royal cheats in leaf-cutting ant societies. Native to Central America, *Acromyrmex echinatior* have massive colonies that cultivate an edible fungus on the leaves that the workers collect and store in a massive subterranean chamber (Hölldobler and Wilson 1990). *A. echinatior* has two different-sized workers, small (SW) which specialise in tending the fungus garden, and large ones (LW) which forage outside the nest for plant material to feed the fungus with.

Queens of *A. echinatior* mate with multiple (haploid) males (Sumner *et al* 2004) and as a result their diploid offspring (queens or workers) consist of a number of full-sister lineages (patrilines). Ants in different patrilines are half-sisters. Hughes and colleagues (Hughes *et al* 2003; Hughes and Boomsma 2007) have already shown that some patrilines have more LW than others, but now Hughes and Boomsma have shown that some individuals of some patrilines are more likely to become queens than individuals of other patrilines. In a truly egalitarian society, all else being equal, an individual of any patriline would have an equal chance of becoming a queen. But like Elizabethan England, it seems individuals of some ant families are more likely to become queens than others.

The use of the term 'cheat' to describe individuals (or genotypes) that act to increase their reproductive output may seem odd to readers not used to thinking about different levels of selection (Keller 1999). In this context it is instructive to think of an insect society as being more analogous to a metazoan body than a human society. Both bodies and insect societies are comprised of a large number of individuals (cells in a metazoan body, workers in an insect colony) that are potentially selfish reproducers, but which are simultaneously dependent on the collective for their survival. Selfish reproduction (cancer or worker reproduction) is good for the reproducer, but very bad for the collective. Hence for social cohesion to be maintained, the collective must evolve systems to control selfish reproduction or reproductive 'cheating' by its parts (Maynard Smith and Szathmáry 1995).

How do the ant larvae cheat? Whether or not a female larva becomes a queen or a worker is determined by an interaction between the larva and adult workers that feed it. The larva signals its potential to become a queen and nurse workers either 'agree' and respond by provisioning the larva with extra food, or not (Wheeler 1991). In the latter scenario the larva becomes a worker, whereas in the former it becomes a queen. A numerical bias towards some patrilines among new queens is a result of variation in the ability of female larvae to signal their 'queen potential'. Hughes and Boomsma show that one fifth of patrilines cheat on their nestmates by having a much higher chance of becoming queens than workers. These royal patrilines are shown to be rare both within individual colonies and in the population as a whole.

Only the royal-SW patrilines are true cheats. 'Normal' patrilines are represented roughly equally among small and large workers and queens, whereas 'royal' patrilines show a bias towards queens and a bias towards either large workers (royal-LW patrilines) or small workers (royal-SW patrilines). As larvae destined to become LW also need to be fed more, the slightly higher than expected contribution of royal-LW patrilines towards queens is most likely a result of larvae of these patrilines 'accidentally' being fed extra to allow them to become queens. These patrilines are equally abundant as 'normal' patrilines within colonies. The 'real' cheats are the royal-SW patrilines, which hardly contribute to the production of

Keywords. Cheating; reproductive parasitism; social insects

workers and if they do, produce mostly SW. Hence, 'accidental' feeding does not explain the bias towards queens in royal-SW patrilines. Royal-SW patrilines were shown to have an increased fitness of almost 500% relative to normal patrilines (determined as their contribution to the next generation of queens), whereas the fitness of royal-LW was not much higher than that of normal patrilines.

Despite the enormous increase in fitness, royal-SW patrilines are rare, as evolutionary theory would predict for real cheats (Keller 1999). Most likely the frequency of cheating genotypes is constrained by colony-level selection: colonies that contain too many royal cheats suffer a reduction in reproductive output. In addition, the direct feeding of ant larvae by workers gives nurse workers some control over caste-fate of larvae by evolving the capacity to recognising potential cheats. However, such recognition will be more error-prone the rarer the cheats are.

Hughes and Boomsma's study has added to an increasing body of evidence that reproductive cheating is widespread in insect societies. In some stingless bee species about 20% of female brood develop into queens, only to be slaughtered by workers as soon as they emerge (Wenseleers *et al* 2005). Female brood can influence their caste fate because larvae develop in sealed cells which have been provided with sufficient food for development before oviposition. Hence, there is no contact between developing brood and nurse workers, allowing brood to express selfish behaviour. That this is against the interest of the colony is evidenced by the mass killing of newly-emerged queens.

The Cape honey bee (*Apis mellifera capensis*) is a unique subspecies of honey bee because its unmated workers are able to produce diploid female offspring via thelytoky (a form of parthenogenesis also known as 'virgin birth') (Onions 1914). Thus, unlike workers of the vast majority of social Hymenoptera where unmated workers can only produce haploid male offspring, workers of the Cape honey bee can compete directly with their queen over maternity of diploid, female offspring. Thus they can contribute to the next generation of new queens. And indeed, workers of the Cape honey bee do contribute to the production of new queens, with almost 60% of all queens being offspring of workers (Jordan *et al* 2008). But this is only part of the story, as over 65% of worker-produced queens were daughters of workers that were not born in that colony. These cheats are true reproductive parasites, as they exploit the host colony at no cost to themselves. Why colonies do not protect themselves against this exploitation is currently unclear.

Reproductive cheating is not restricted to producing royalty. It includes anarchistic honey bees in which workers of some patrilines lay male-producing (haploid) eggs despite the presence of the queen and at an obvious cost to the colony (Oldroyd *et al* 1994), and parasitic bumble bee (Lopez-Vaamonde *et al* 2004) and honey bee (Nanork *et al* 2005) workers which enter other nests and dump male-producing eggs there. Thus although the social insects are still impressive examples of cooperative societies, we now know that their social cohesion depends very much on policing mechanisms that keep selfish behaviour at bay.

On reflection, perhaps Shakespeare was right after all, and insect colonies are rather similar to our own societies.

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*e*Publication: 24 April 2008