



Individual and genetic task specialization in policing behaviour in the European honeybee



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Cooperation in biological systems is frequently maintained by social enforcement mechanisms, where individually egoistic and group-costly behaviour is mutually suppressed by other group members. One of the best examples in nature is worker policing in the honeybee, *Apis mellifera*, where workers selectively remove or 'police' eggs laid by workers that egoistically try to produce their own offspring instead of working for the good of the colony. It has long been suggested that worker policing behaviour should be genetically determined, as theory has shown that queen polyandry in the honeybee would be expected to give rise to clear indirect genetic or 'inclusive fitness' benefits of worker policing, thereby causing genes for policing to spread in the population. In the present study, we tested the theory that worker policing should have a genetic component by determining whether workers belonging to different patrilines, derived from different fathers, differ in their tendency to police eggs. This analysis showed that variation in policing behaviour indeed has a genetic basis, with the trait having an estimated broad-sense heritability of 0.25 ([0.013–0.46] 95% confidence limits). In addition, there was clear individual specialization in policing, as just a few individuals within each patriline were observed to police. Remarkably though, there was no evidence for age specialization, as workers of all ages, except those younger than 10 days and older than ca. 40 days, engaged in policing. This contrasts with most other behaviours in the honeybee, which usually follow a strict age-linked pattern of division of labour. Overall, we conclude that worker policing behaviour in the honeybee is genetically heritable and that workers of all ages engage in policing to help maintain the social order in the colony.

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In the evolution of life on earth, natural selection has resulted in several so-called 'major transitions in evolution', where previously independently reproducing units teamed up, in some cases even giving rise to 'obligate cooperation', where the higher entities lost the ability to reproduce without the help of their subunits (Bourke, 2011; Maynard Smith & Szathmary, 1995). Examples include the cooperation between previously independently reproducing bacteria in the origin of the eukaryotic cell, the joining up of cells in the

origin of multicellular organisms, and the cooperation between individuals in highly advanced societies, such as those of the social insects (Maynard Smith & Szathmary, 1995; Queller & Strassmann, 2009). The long-term maintenance of cooperation in these systems, however, frequently requires social coercion and mutual policing mechanisms in order to suppress conflict caused by the expression of individually selfish but group-costly behaviour (Frank, 2003; Rainey & De Monte, 2014; Ratnieks, Foster, & Wenseleers, 2006; Ratnieks & Wenseleers, 2008).

A prime example of such conflict-reducing policing behaviour occurs in several independently evolved lineages of social insects, including honeybees, ants, wasps and bumblebees, and is known as 'worker policing'. Worker policing is the behaviour where workers selectively destroy eggs laid by 'rogue' workers that, instead of helping to rear the queen's brood, decide to try to reproduce by depositing unfertilized, male-destined eggs (Ratnieks & Visscher,

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1989; Wenseleers & Ratnieks, 2006a). Worker reproduction can be in the genetic interests of individual workers, as each is more related to its own sons ($r = 0.5$) than to the sons of the queen (brothers, $r = 0.25$) (Ratnieks et al., 2006; Wenseleers, Helantera, Hart, & Ratnieks, 2004). Yet, theory also predicts that collective workers' interests should frequently oppose such individually egoistic behaviour, and that workers can be selected to try to prevent other workers from reproducing, either by attacking workers with developed ovaries (e.g. Dampney, Barron, & Oldroyd, 2002; Visscher & Dukas, 1995) or by eating eggs laid by other workers (reviewed in Wenseleers & Ratnieks, 2006a).

The reasons that worker policing behaviour can be selected for are varied, and at a theoretical level this behaviour can be caused by worker reproduction resulting in too many males being reared (Foster & Ratnieks, 2001b), worker male production being traded off against long-term colony growth, (Ohtsuki & Tsuji, 2009; Ratnieks, 1988; Wenseleers, Helantera, Alves, Duenez-Guzman, & Pamilo, 2013), reproductive workers working at a reduced rate (Dampney, Barron, & Oldroyd, 2004; Wenseleers, Helantera et al., 2004; but see Naeger, Peso, Even, Barron, & Robinson, 2013), worker-laid eggs being less viable than queen-laid ones (Pirk, Neumann, Hepburn, Moritz, & Tautz, 2004; but see Beekman & Oldroyd, 2005; Helantera, Tofilski, Wenseleers, & Ratnieks, 2006), workers obtaining direct reproductive benefits from policing ('selfish worker policing', Bonckaert et al., 2011; Saigo & Tsuchida, 2004; Stroeymeyt, Brunner, & Heinze, 2007; Wenseleers, Tofilski, & Ratnieks, 2005), worker policing being targeted against genetically unrelated worker reproductive parasites (Beekman & Oldroyd, 2008; Pirk, Neumann, & Hepburn, 2007; Zanette et al., 2012), or workers obtaining indirect genetic benefits if the colony kin structure is such that workers are less related to the sons of other workers (nephews) than to the sons of the queen (brothers) (Ratnieks, 1988; Starr, 1984; Wenseleers & Ratnieks, 2006a; Wenseleers, Tofilski et al., 2005).

This last theory, which is based on the presence of indirect genetic or 'inclusive fitness' benefits (Hamilton, 1964) and is known as the relatedness theory of worker policing, has perhaps received most attention, and applies when the mother queen is mated to two or more males or when the colony is headed by several related queens (Ratnieks & Wenseleers, 2008). The classic example is the honeybee, *Apis mellifera*, where queens mate with about 10 males, which causes workers to be genetically more related to the queen's sons (brothers, $r = 0.25$) than to the sons of other workers (a mix of full- and half-nephews, $r = 0.15$) and where, as predicted, workers effectively police any eggs laid by other workers (Ratnieks & Visscher, 1989) or attack workers with developed ovaries (Dampney et al., 2002; Visscher & Dukas, 1995). Similar behaviour has been observed in many other social insect species, including in ants (e.g. D'Ettorre, Heinze, & Ratnieks, 2004; Dijkstra, van Zweden, Dirchsen, & Boomsma, 2010; van Zweden, Fürst, Heinze, & D'Ettorre, 2007), wasps (e.g. Bonckaert et al., 2008; Foster & Ratnieks, 2001a; Oi et al., 2015; Wenseleers, Tofilski et al., 2005), bumblebees (Zanette et al., 2012) and Asian honeybees, *Apis cerana* (e.g. Oldroyd et al., 2001), and, as predicted, has been shown to be disproportionately common in species in which collective relatedness disfavours worker reproduction (Wenseleers & Ratnieks, 2006a). Effective policing has also been shown to act as a deterrent against attempting to reproduce (Wenseleers, Hart, & Ratnieks, 2004; Wenseleers, Helantera et al., 2004; Wenseleers & Ratnieks, 2006b). In the honeybee, for example, more than 98% of all worker-laid eggs are eaten by other workers (Ratnieks & Visscher, 1989) and, consequently, only about one in 10 000 workers develop their ovaries in the presence of the queen (Ratnieks, 1993).

Although worker policing behaviour in the honeybee is cited in all major behavioural ecology textbooks as providing classic

support for the theory of inclusive fitness (Davies, Krebs, & West, 2012; Dugatkin, 2009), and the logic that a gene for worker policing would be expected to spread in honeybee populations due to indirect genetic benefits is undeniable, it remains entirely untested to what extent policing behaviour does indeed have a genetically heritable basis. In fact, hardly any detailed observational studies have been published about honeybee policing behaviour. This contrasts with the detailed and generally available knowledge about division of labour in the honeybee which appears to be partly genetically based and partly linked to age ('age polyethism'; e.g. Calderone & Page, 1988; Hunt, Page, Fondrk, & Dullum, 1995; Johnson, 2010; Oldroyd & Thompson, 2006; Oxley, Spivak, & Oldroyd, 2010; Robinson, 1992; Robinson & Page, 1989; Seeley, 1995; Smith, Toth, Suarez, & Robinson, 2008; Winston, 1987). In the honeybee, genetic control typically expresses itself in large differences between patriline in the degree to which workers engage in carrying out a particular task (Calderone & Page, 1988; Oldroyd & Fewell, 2007; Oldroyd & Thompson, 2006), which has, for example, been shown in the context of specialization in pollen versus nectar foraging (e.g. Hellmich, Kulincevic, & Rothenbuhler, 1985), undertaking and guarding (e.g. Robinson & Page, 1988; Trumbo, Huang, & Robinson, 1997) or hygienic behaviour towards dead brood (e.g. Pernal, Sewalem, & Melathopoulos, 2012).

The aim of this study was two-fold. First, we carried out detailed behavioural observations of honeybee policing behaviour using a newly developed observation hive set-up and quantified the degree to which policing behaviour varies across different patrilines. In this way, we were able to infer whether honeybee policing is indeed partly genetically heritable (Ratnieks, 1988). Second, we determined whether, within each patriline, individual workers also specialize in carrying out policing behaviour, and whether, as is generally the case for other tasks in honeybees (Seeley, 1982), the expression of policing behaviour is restricted to a particular age cohort. Previously, individual task specialization in policing has been demonstrated in only a handful of species (in the ants *Pachycondyla inversa* (van Zweden et al., 2007) and *Platythyrea punctata* (Barth, Kellner, & Heinze, 2010) and the vespine wasp *Dolichovespula norwegica* (Bonckaert et al., 2011), but age specialization has not been investigated in any of these. Finally, we linked the results we obtained to adaptive theories on optimal task allocation and division of labour in insect societies (Duarte, Weissing, Pen, & Keller, 2011; Goldsby, Dornhaus, Kerr, & Ofria, 2012).

METHODS

Observation Hive Set-up

Experiments were performed at the beekeeping facility of the University of Ghent (Belgium) in 2009 and were then replicated once more at the beekeeping facility of the KU Leuven (Belgium) in 2010. Below, we refer to these colonies as colonies 1 and 2. In each year, a colony of *A. m. carnica* with a naturally mated queen was housed in a three-frame observation hive kept inside at room temperature (Fig. 1a). The observation hive was connected to the outside via a plastic tube to allow bees to forage freely. The queen was not restricted in any way, but brood was removed regularly before bees emerged. Each day, we marked 100 newly emerged bees individually using a combination of numbered bee tags (Opalithplättchen, Graze, Weinheim, Germany, and Ewa Podlowska, Fabianki, Poland) and acrylic paint marks on their abdomens (Amsterdam All Acrylics, standard series, Royal Talens, Apeldoorn, The Netherlands, and deco craft, Lefranc & Bourgeois, Le Mans, France). These bees were offspring of an unrelated, naturally mated queen and were obtained by placing a sealed brood comb in an incubator at 34 °C under high relative humidity, after which all

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