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Collective personalities in honeybee colonies are linked to colony fitness

Margaret K. Wray [a,*], Heather R. Mattila [b,1], Thomas D. Seeley [a]

[a] Department of Neurobiology and Behaviour, Cornell University
[b] Department of Biological Sciences, Wellesley College

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Personality differences (i.e. consistent between-individual differences in behaviour) play an important role in the lives of humans and other animals, influencing both their day-to-day actions and their long-term reproductive success. For organisms living in highly structured groups of related individuals, such as colonies of social insects, personalities could also emerge at the group level. However, while numerous recent studies have investigated individual-level personality, the phenomenon of collective personality in animal groups has received little attention. In this paper, we apply the concept of collective personality to colonies of honeybees (*Apis mellifera*). We document the presence of consistent differences among colonies across a wide range of collective behaviours and demonstrate a link between colony-level personality traits and fitness. The colonies in our study showed consistent behavioural differences in traits such as defensive response, foraging activity and undertaking, and several of these traits were correlated as part of a behavioural syndrome. Furthermore, some of these traits were strongly tied to colony productivity and winter survival. Our results show that the concept of collective personality is applicable to colonies of social insects, and that personality differences among colonies can have important consequences for their long-term survival and reproduction. Applying the concept of personality to close-knit animal groups can provide important insights into the structure of behavioural variability in animal populations and the role that consistent between-group behavioural differences play in the evolution of behaviour.
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Personality differences can have profound effects on the behaviours and long-term fitness of individual organisms. Human psychologists have long recognized that people consistently differ in their responses to different situations (Allport 1937; Mischel & Shoda 1995), and that personality traits can affect reproductive success (Eaves et al. 1990). More recently, studies have shown that nonhuman animals also display consistent, heritable differences in personality traits such as boldness, tendency to explore and aggressiveness (Wilson 1998; Gosling 2001; Bell et al. 2009) and that these traits can be linked to survival and reproductive success (Dingemanse & Réale 2005; Smith & Blumstein 2008).

The word 'personality' is typically used to refer to consistent behavioural differences among individual organisms. However, to the extent that cooperative groups differ from one another in their collective behaviours, these groups can also be thought of as having 'collective personalities' (Stewart 2003). In humans, for example, studies of collective personality have shown that some groups tend to be more communicative or more aggressive than others (Hofmann & Jones 2005), just as some individuals are more extroverted or less agreeable than others. These collective personality differences can have important effects on a group's ability to survive and function. In human organizations and teams, for instance, collective personality can affect a group's performance (Stewart 2003; Hofmann & Jones 2005) and its ability to attract additional members (Anderson et al. 2010).

The concept of collective personality has been applied primarily to human social groups, but this idea is also relevant to many animal groups, especially cooperative groups of related individuals whose genetic interests are aligned. In a social insect colony, for example, workers' actions are so well coordinated that the colony behaves as a single 'superorganism' (Hölldobler & Wilson 2008) and nearly all reproduction occurs at the colony level, either during colony fissioning or when males and queens leave to found new colonies. In such groups, any fitness consequences of collective personality should be especially apparent because natural selection operates primarily on differences among colonies (between-group selection) rather than among individuals within a colony (within-group selection) (Korb & Heinze 2004; Bergmüller et al. 2007).

* Correspondence: M. Wray, Department of Neurobiology and Behavior, Cornell University, W302 Mudd Hall, Ithaca, NY 14853, U.S.A.
E-mail address: mkk29@cornell.edu (M.K. Wray).
[1] H. Mattila is at the Department of Biological Sciences, Wellesley College, E118 Science Center, 106 Central Street, Wellesley, MA 02481, U.S.A.

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Previous work suggests that social insect colonies often differ in their collective behaviour. Beekeepers claim that 'every colony of honeybees has an individual character' (Weiss 1983, page 133), and breeders of honeybees (*Apis mellifera*) report marked differences in the productivity and temperament of their colonies (Laidlaw 1979; Laidlaw & Page 1997). Numerous studies have shown that honeybee colonies differ in traits such as defensive response (e.g. Collins et al. 1982; Breed 1991; Hunt et al. 1998; Guzmán-Novoa et al. 2002a, b), hygienic behaviour (e.g. Rothenbuhler 1964; Arathi & Spivak 2001) and pollen hoarding (e.g. Hellmich et al. 1985; Pesante et al. 1987). Several of these differences in colony-level behaviour are consistent across multiple rounds of testing (e.g. Giray et al. 2000; Guzmán-Novoa et al. 2003), and some studies have found correlations between one or more of these behaviours (e.g. Page et al. 1995a; Giray et al. 2000; Guzmán-Novoa et al. 2002a).

Taken together, these findings suggest that the concept of collective personality is highly relevant to the study of colony-level behaviour in social insects. However, relatively few studies have quantified the range of behavioural variation that characterizes colonies of European honeybees with naturally mated queens; most previous studies involved both Africanized and European bees or used colonies from artificially selected genetic lines (although see Breed & Rogers 1991). Furthermore, we know very little about the relationship between these collective behavioural traits and colony-level fitness.

Our study expands on prior results by applying the concept of collective personality to social insects and exploring the link between colony-level personality and fitness. We established 25 equally sized honeybee colonies in empty hives, assessed the consistency of their responses to a variety of colony-level behavioural tests, and monitored their subsequent growth and survival to determine whether any of these behavioural traits were linked to colony fitness. Observing our colonies from the colony-founding stage allowed us to equalize their size, weight and physiological state, and provided them with a demanding test of fitness. In temperate climates, only 24% of newly founded colonies survive their first winter (Seeley 1978), so forcing colonies to found new nests encouraged high levels of productivity and emphasized performance differences among colonies. Furthermore, by testing the same colonies on a variety of behavioural tests, we were able to determine whether these colony-level traits formed suites of correlated behaviours, or 'behavioural syndromes' (Sih et al. 2004a, b). In individual animals, behavioural syndromes involving personality traits like activity, aggression and boldness vary across populations according to ecological factors like the level of predation (Bell 2005; Dingemanse et al. 2007), and are thus likely to be adaptive.

METHODS

Study Colonies

On 20 May 2009, we created 25 artificial swarms from genetically unrelated colonies of European honeybees with naturally mated queens. We created each swarm by transferring 1 kg of workers (~7500 bees) and their mother queen from a single colony to a screened wooden swarm cage using standard methods (Seeley & Visscher 1985). Caged bees were fed 1:1 sucrose solution ad libitum for 3 days to induce the physiological state of bees in a natural swarm. On the evening of 23 May, we installed each swarm in an 8-frame full-depth Langstroth hive body with alternating frames containing full and partial sheets of wax foundation. Colonies were housed in the same apiary, at the Liddell Field Station of Cornell University in Ithaca, New York (42°26′N, 76°30′W). Hives were arranged in four rows, with adjacent hives at least 2 m apart to minimize drifting of bees.

During the course of the study, some colonies constructed enough comb to nearly fill their hives. An additional hive body was added to any colony that had built comb filling approximately 90% of its hive.

All colonies received standard treatments against Varroa mites (Apistan®) in April and against American Foulbrood (Terra Pro, Walter T. Kelley Co., Clarkson, KY, U.S.A.) in late June.

Behavioural Tests

We performed behavioural tests to assess each colony's level of defensive response and foraging activity, the diversity of pollen its foragers collected, and its workers' tendency to repair damaged comb ('comb repair'), run across comb ('runniness') and remove dead bees from the hive ('undertaking').

Testing schedule

To ensure that behavioural differences among colonies were not due to variations in colony weight or population size, all tests were performed during the first 5 weeks of the study, before colonies had reared new foragers or gained significant weight. Each colony was also checked periodically to confirm that its queen was healthy and laying well.

To assess the consistency of each colony's response, we tested colonies six times at approximately weekly intervals: on 25–26 May, 31 May–1 June, 6–7 June, 13–14 June, 17 and 19 June (it rained on 18 June), and 26–27 June. Each round of tests lasted 2 days. On day 1, we measured each colony's level of foraging activity, collected pollen foragers to assess pollen diversity, and added 100 dead bees to each hive in the evening. On day 2, we assessed the colonies' undertaking speeds and measured colonies' runniness and defensive response. The schedule for comb repair measurements is described below.

Foraging activity

On the first day of each round of tests, we measured colonies' foraging activity at three times: morning (0830–1000 hours), midday (1300–1430 hours) and evening (1800–1930 hours). At each time, observers counted the total number of bees entering the hive and the number entering with pollen during four 1-min intervals. The average of these 12 measurements provided a measure of each colony's daily foraging activity. We used the average total number of returning bees as our measure of foraging activity, as this was strongly correlated with the number of returning pollen foragers ($r = 0.896$, $P < 0.0001$). During each 1 min interval, two colonies were monitored simultaneously by two different observers, following a randomized order that was determined using a random number generator (http://www.randomizer.org/).

Pollen diversity

We measured each colony's pollen diversity by capturing approximately 30 returning pollen foragers from each colony and counting how many different colours of pollen they carried. We collected pollen foragers on the first day of testing, immediately following the morning measure of foraging activity (1030–1215 hours).

We collected pollen foragers from five colonies at a time by screening off each hive's entrance and transferring returning pollen foragers to a screened cage ($7 \times 6 \times 6.5$ cm) until 30 foragers had been collected or 45 min had passed. Collected foragers were anaesthetized with CO_2 and frozen. Later that day, one person (M.K.W.) separated pollen foragers into groups according to pollen colour, and a second person (H.R.M.) reviewed these groupings. In the event of disagreement, we combined foragers into a single

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