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Automated monitoring reveals extreme interindividual variation and plasticity in honeybee foraging activity levels

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Workers in many eusocial insect species show a phenomenon sometimes referred to as 'elitism', in which a small proportion of individual workers engaged in a task perform a disproportionately large fraction of the work achieved by the colony as a whole. This phenomenon has not been well studied for foraging behaviour in honeybees (*Apis mellifera*) because detailed observational studies of foraging activity have been limited by the difficulty of successfully tracking large numbers of individual workers. Here, we used radio frequency identification technology to monitor honeybee flight behaviour automatically and generate lifetime flight activity records for large numbers of individuals from multiple colonies. We observed a consistent skew in activity levels of honeybee foragers, similar to that reported in many other social insects. However, this skew was a consequence of modulation of foraging activity by environmental and social factors rather than the existence of a distinct group or subcaste of elite foragers. Individual responses to experimental manipulation of the foraging workforce confirmed that activity level was flexibly adjusted according to colony needs. These results demonstrate that elitism in insect societies can arise as the extreme of a stable spectrum of individual behavioural activity that allows the colony to respond easily to unexpected needs rather than relying on responses of a rigidly defined subgroup of workers.

Chaucer's *Canterbury Tales* quotation 'busy as a bee' mirrors an assumption made in early models of eusocial insect behaviour: that workers specializing on a given behavioural task display similar or identical rates of task performance. Because eusocial insect colonies are composed largely of genetically related workers and because reproductive fitness is determined at the level of the colony, variation in performance among workers within a colony had no obvious origin or possible advantage. In reality, for a wide range of species and behaviours, individual workers show great variation in activity levels (Beverly, McLendon, Nacu, Holmes, & Gordon, 2009; Dornhaus, 2008; Hurd, Nordheim, & Jeanne, 2003; Möglich & Hölldobler, 1974; O'Donnell & Jeanne, 1990; Oster & Wilson, 1979; Pendrel & Plowright, 1981; Plowright & Plowright, 1988; Robson & Traniello, 1999). The term elitism has been used to describe the phenomenon in which a subset of the individuals performing a given task show a higher activity level than the others (Oster & Wilson, 1979).

Several explanations have been proposed for the adaptive value of variation in activity level within the set of individuals performing a task. Individuals with lower activity may represent a reserve workforce, enabling the colony to respond rapidly to sudden and unpredictable demands or opportunities (Plowright & Plowright, 1988). Alternatively, individuals within a workforce may have behavioural specializations that make them more or less able to perform a task efficiently (Oster & Wilson, 1979). It is likely that the factors promoting variation in activity level are different for different species, or even for different tasks performed by a single species.

Despite a vast body of literature devoted to foraging behaviour of honeybees (*Apis mellifera*), reports of systematic studies of elitism in honeybee foragers are absent. Only a few studies in the last half century have alluded to elite forager honeybees. Sekiguchi and Sakagami (1966) described the presence of a few individual honeybee foragers with unusually high flight activity relative to

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other foragers from the same colony. Ribbands (1953) also reported a maximum of 150 trips in a single day made by individual nectar foragers to an artificial feeder. These findings indicate the potential for great variation in activity level within a colony's foraging population. To our knowledge, no prior study has investigated whether elite honeybee foragers represent a distinct subgroup, how the tendency to extreme foraging activity might change over the individual life span, or how foraging elitism relates to colony-level regulation of foraging activity.

One likely reason that these types of questions have not been previously explored in honeybees is the difficulty of monitoring flight activity. The type of continuous manual observation and recording of individual behaviour that would be required is a significant challenge. The recent appearance of technologies that enable automated detection of individual insects and other small animals has presented the means to pursue research that previously faced these obstacles.

In this study, we adapted existing radio frequency identification (RFID) tagging technology, along with custom-written recording software and analysis algorithms to track the lifetime flight activity of several hundred individuals in several different colonies of honeybees. RFID microtransponder tags have been used several times over the last 10 years (Molet, Chittka, Stelzer, Streit, & Raine, 2008; Robinson, Richardson, Sendova-Franks, Feinerman, & Franks, 2009; Robinson, Smith, Sullivan, & Franks, 2009; Streit, Bock, Pirk, & Tautz, 2003; Sumner, Lucas, Barker, & Isaac, 2007) to track the entry and exit of bees, wasps or ants from the nest. RFID tags have also been used to monitor the long-term exploratory behaviour and locomotor activity of mice in a seminaturalistic environment (Freund et al., 2013; Lewejohann et al., 2009). RFID tags are small, light weight and robust, they can be coded with many unique IDs and they are economical enough to allow for many individuals to be monitored simultaneously. These characteristics make them a particularly good choice for studies with honeybees; RFID tags already have been used successfully in studies of honeybee navigation and homing behaviour (Core et al., 2012; Decourtye et al., 2011; He et al., 2013; Henry et al., 2012; Pahl, Zhu, Tautz, & Zhang, 2011).

Our use of RFID technology allowed us to analyse the flight activity of a large sample of individually identified bees over an extended period. This large data set allowed us to confirm the existence of a spectrum of activity levels among honeybee foragers, from relatively inactive to highly active. We investigated potential differences between high-activity foragers and other foragers within the same colony. We also examined the effect of the removal of high-activity foragers on the activity levels of remaining tagged individuals in the colony's foraging population. Our results demonstrate that individuals with high ('elite') foraging activity represent the extreme of a continuum of activity levels. However, we also found that honeybee foragers can adjust their foraging activity in response to changes in the foraging workforce, including a rapid assumption of high-foraging activity status.

METHODS

Monitoring Technology

Bees were tagged with laser light-activated 'p-chip' microtransponders (tags) (PharmaSeq, Princeton, NJ, U.S.A.). The tags were detected by laser readers (PharmaSeq) connected via a USB cable to a computer. Each tag carried a unique identification number; the tag's upper surface contains photocells that, when lit by a reader's red laser beam, activate the chip to transmit its ID for a distance of up to 10 mm to a pickup coil in the head of the reader. Processing and decoding of the ID were performed with firmware and p-Chip Reader software provided by PharmaSeq.

Figure 1. Typical positioning of two PharmaSeq p-chip microtransponders on the thorax of an adult worker honeybee.

Because of the small 1.5 mm diameter of the laser beam, two tags were attached to a bee to increase the likelihood of detection (Fig. 1). Each tag was 500 × 500 × 100 μm with a weight of 90 μg; two tags fit easily on the thorax of the bee, and their combined weight was only 0.56% of the average load carried by a nectar forager (Winston, 1987). This means that it is unlikely that the presence of the tags impaired natural foraging behaviour.

To read tagged bees, a 10 × 10 mm plastic tube walkway was attached to the hive entrance, with two laser readers projecting into the top of the tube (Fig. 2). Bees passed sequentially under each reader as they entered and exited the hive, so that the order of detection by each reader could be used to infer the direction of travel. The top and sides of the walkway were coated with Fluon (Bioquip Products, Rancho Dominguez, CA, U.S.A.) while the floor of the walkway had numerous small drilled holes to provide grip; this encouraged most bees to walk on the floor of the walkway, maximizing the probability that their tags would be detected. Upon

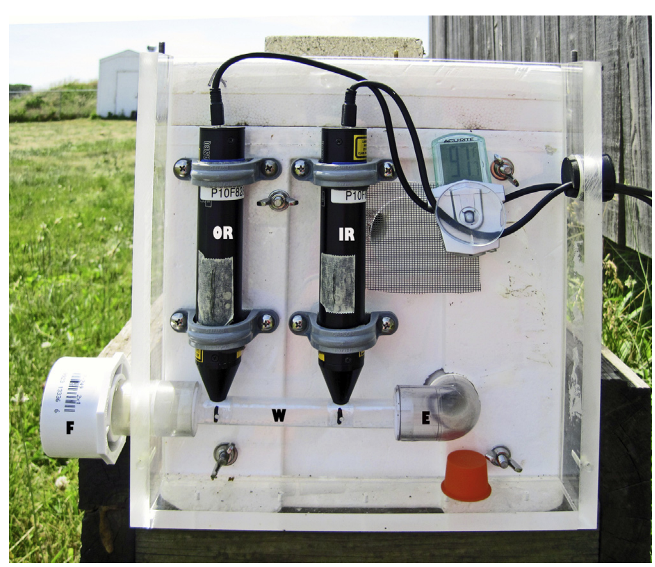

Figure 2. Recording apparatus attached to the front of a six-frame nucleus hive. Bees leave the hive through a 90° entrance elbow (E), then pass through a 10 mm square walkway (W) exiting to the outside at the funnel (F). Outer (OR) and inner (IR) readers record bees passing in the walkway underneath. A ventilated Plexiglas cover fits over the apparatus for rain protection.