Animal Behaviour 87 (2014) 91–96

Contents lists available at ScienceDirect

Animal Behaviour

journal homepage: www.elsevier.com/locate/anbehav

Cognition across castes: individual recognition in worker *Polistes fuscatus* wasps

Allison Injaian, Elizabeth A. Tibbetts*

Department of Ecology and Evolutionary Biology, University of Michigan, Ann Arbor, MI, U.S.A.

ARTICLE INFO

Article history:
Received 4 June 2013
Initial acceptance 16 July 2013
Final acceptance 2 October 2013
Available online 14 November 2013
MS. number: A13-00476R

Keywords:
individual recognition
intraspecific variation
paper wasp
Polistes fuscatus
social behaviour

In many signalling systems, intraspecific variation in recognition abilities is based on developmental stage, experience or caste. However, the occurrence of intraspecific variation in recognition has not been thoroughly examined in species with individual recognition. For example, previous work has shown that individual recognition is an important aspect of the social life of *Polistes fuscatus* (paper wasp) nest-founding queens, as individual recognition stabilizes dominance interactions and reduces aggression. To date, the potential for individual recognition among *P. fuscatus* workers has been largely ignored. Here, we explore whether there is intraspecific variation in individual recognition by testing *P. fuscatus* worker recognition abilities in a series of staged contests. The results indicate that *P. fuscatus* workers are capable of individual recognition: focal workers paired with previously encountered partners experienced significantly less aggression and more nonaggressive bodily contact than focal workers paired with unknown social partners. We propose two potential explanations for individual recognition among workers: (1) worker individual recognition may be favoured because it provides social benefits to workers, or (2) worker individual recognition may be a byproduct of selection for individual recognition in foundresses. Individual recognition is often considered a cognitively challenging form of recognition, so future studies that compare the sophistication of recognition across castes will be useful to assess whether there are more subtle differences in cognitive abilities or recognition behaviour between *P. fuscatus* nest-founding queens and workers.

Animals exhibit a range of recognition behaviours, including species, gender, kin, mate and individual recognition (Sherman, Reeve, & Pfennig, 1997). Individual recognition is a relatively precise form of recognition where each social partner is identified through its unique phenotype (Dale, Lank, & Reeve, 2001; Tibbetts & Dale, 2007). Individual recognition is typically considered to be more cognitively complex than many other forms of recognition as it requires organisms to learn and remember the distinctive phenotypes of multiple conspecifics (Barnard & Burk, 1979). Despite this cognitive complexity, individual recognition is taxonomically widespread, occurring in mammals, birds, lizards, crustaceans and insects (Falls, 1982; Gherardi, Cenni, Parisi, & Aquiloni, 2010; Glinski & Krekorian, 1985; Sugita, 2007; Tibbetts, 2002). Individual recognition is also an important factor in many social behaviours, including monogamy, dominance hierarchies and reciprocal altruism (Barnard & Burk, 1979; Muller, Eggert, & Elsner, 2003; Trivers, 1971).

To date, most research on individual recognition has focused on identifying species that are capable of individual recognition, without assessing whether there is intraspecific variation in recognition abilities (Brooks & Falls, 1975; Hurst et al., 2001; Irvine, 1998). Intraspecific variation in recognition abilities may commonly occur when some receivers are less capable of recognition than others (Reeve, 1989). For example, intraspecific variation in kin recognition of red-legged frogs, *Rana aurora*, is based on developmental stage, with recognition abilities present during larval stages and lost in later life stages (Blaustein & O'Hara, 1986). Intraspecific variation in recognition may also be based on experience. For example, juvenile Barbary macaques, *Macaca sylvanus*, cannot distinguish between group and nongroup conspecifics, but adults are capable of group discrimination (Schell, Rieck, Schell, Hammerschmidt, & Fischer, 2011). Finally, previous work suggests that recognition abilities may commonly vary with caste. For example, nestmate recognition in leaf-cutting ants, *Atta vollenweideri*, varies among worker subcastes, with foraging workers showing increased nestmate recognition relative to other worker subcastes (Kuebler, Kelber, & Kleineidam, 2010). Given the

* Correspondence: E. A. Tibbetts, Department of Ecology and Evolutionary Biology, University of Michigan, 2063 Kraus Natural Science Building, 830 N. University, Ann Arbor, MI 48109, U.S.A.
E-mail address: tibbetts@umich.edu (E. A. Tibbetts).

0003-3472/$38.00
http://dx.doi.org/10.1016/j.anbehav.2013.10.014

prevalence of intraspecific variation in recognition across species and signalling systems, it may also occur in species with individual recognition.

In the present study, we examined the occurrence of intraspecific variation in individual recognition by testing individual recognition across castes in *Polistes fuscatus* paper wasps. Previous work has shown that *P. fuscatus* nest-founding queens have variable facial patterns that are used for individual recognition (Tibbetts, 2002). Queens are quite adept at individual recognition, as they remember individual conspecifics after a separation of at least 1 week, even if they are living in a complex social environment with multiple other individuals (Sheehan & Tibbetts, 2008). *Polistes fuscatus* queens also have cognitive specialization for individual face recognition, as they learn faces faster and more accurately than other types of visual stimuli (Sheehan & Tibbetts, 2011). Much less is known about the extent of individual recognition in worker *P. fuscatus*. Tibbetts (2002) found that workers, which also have highly variable facial patterns (Fig. 1), are likely capable of individual face recognition, although the pattern was only significant with a one-tailed statistical analysis. There have been no previous tests of individual recognition and memory in *P. fuscatus* workers.

It is difficult to predict the extent of individual recognition in *P. fuscatus* workers. Previous experimental and comparative work suggests that individual recognition evolved to reduce costly aggressive interactions among nest-founding queens (foundresses) (Sheehan & Tibbetts, 2009; Tibbetts, 2002). Behavioural experiments have shown that foundresses that provide unique identity signals receive substantial social benefits, such as decreased aggression within foundress groups, compared with social benefits for unrecognizable foundresses (Sheehan & Tibbetts, 2009). Furthermore, comparative analyses indicate that the type of variable facial patterns used during social signalling are only found in paper wasp species that form cooperative foundress associations, suggesting that signals of individual identity are favoured because of social benefits in the founding stage (Sheehan & Tibbetts, 2010; Tibbetts, 2004).

Although individual recognition is important among foundresses, there is no evidence that workers use individual recognition during social interactions or that workers benefit by being individually recognizable. In stable colonies, workers in *Polistes* and other social insects identify the dominant queen through chemical profiles associated with egg laying (Pfennig, Gamboa, Reeve, Reeve, & Ferguson, 1983; Tibbetts & Sheehan, 2013). Social interactions in stable colonies with queens are unlikely to require individual recognition, as individual recognition is quite rare in social insects (Krasnec & Breed, 2012). If individual recognition is less important during the social lives of workers than it is among foundresses, workers may be less able to learn and remember individual conspecifics than they are foundresses (Tibbetts, 2002). At the same time, *Polistes* are primitively eusocial insects: they lack discrete pre-imaginal castes (Michener, 1969, 1974; O'Donnell, 1998). Queens and workers appear morphologically similar, and their behaviour is flexible (Reeve, 1991). For example, although most of the first brood to emerge on a nest are nonreproductive foragers (workers), a few start their own nests or enter early diapause and emerge the following year as nest-founding queens (O'Donnell, 1996). There may be sufficient overlap between foundresses and workers such that workers are capable of individual recognition, even if individual recognition is not specifically favoured in the worker context.

In this study, we tested individual recognition in *P. fuscatus* workers through a series of staged contests between wasps. Similar methods have been used previously to test individual memory in *P. fuscatus* and to demonstrate a lack of individual recognition in *Polistes dominulus* and *Polistes metricus* (Sheehan & Tibbetts, 2008, 2010). The method was originally developed to measure individual recognition via cuticular hydrocarbons in *Pachycondyla villosa* ants (Dreier, van Zweden, & D'Ettorre, 2007) and was later used to illustrate that *Lasius niger* are unable to recognize individual conspecifics (Dreier & D'Ettorre, 2009). If *P. fuscatus* workers are capable of individual recognition, then we predicted that workers would treat known and unknown rivals differently. Specifically, we predicted more aggression and fewer nonaggressive interactions (positive social behaviour) between wasps during their first meeting than during subsequent social interactions (Dreier et al., 2007; Sheehan & Tibbetts, 2008).

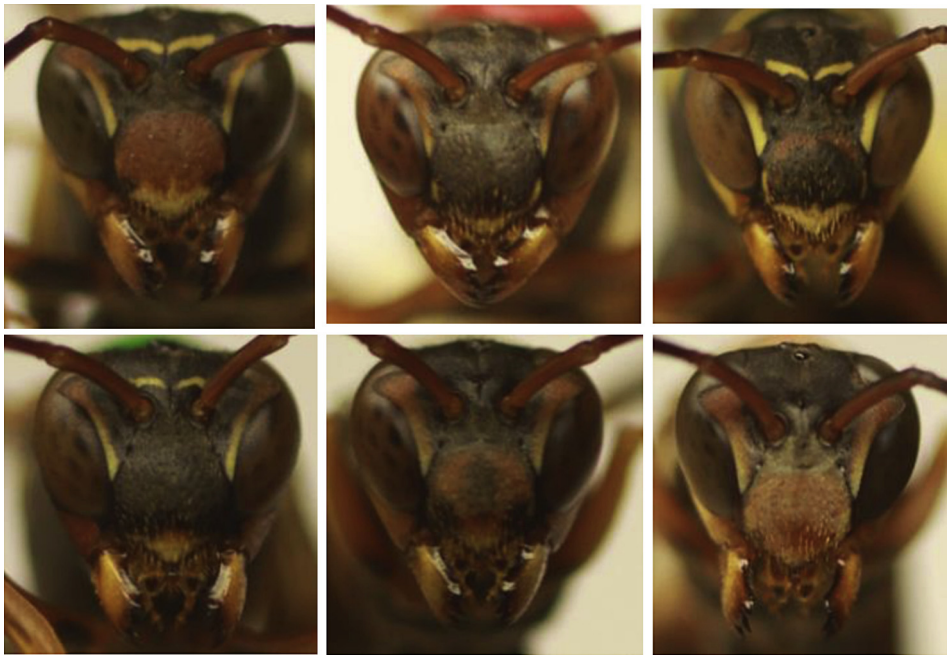

Figure 1. Portraits of *P. fuscatus* workers collected in areas surrounding Ann Arbor, Michigan, U.S.A. Facial variation occurs on the clypeus, eyebrow and inner eye.