



Nestmate discrimination based on familiarity but not relatedness in eastern carpenter bees



J.L. Vickruck*, M.H. Richards

Department of Biological Sciences, Brock University, 1812 Sir Isaac Brock Way, St. Catharines, Ontario, Canada

ARTICLE INFO

Keywords:

Aggression
Cooperation
Nestmate provisioning
Observation nest
Social group formation
Trophallaxis

ABSTRACT

How animals recognize conspecific individuals has important outcomes in many contexts, but interactions among group members are particularly important. Two recognition criteria are often implicated in these interactions: kin recognition is based on relatedness cues and nestmate recognition is based on familiarity. For social insects, both types of recognition are possible, as many nestmates are close kin and familiarity can develop among individuals that encounter each other repeatedly. To discern whether social insects use kin or nestmate recognition, it is necessary to simultaneously assess how relatedness and familiarity influence behaviour. The facultatively social eastern carpenter bee, *Xylocopa virginica*, offers an excellent opportunity to study how either nestmate or kin recognition (or both) may influence interactions among nestmates, as many females disperse from their natal nests in spring, and often attempt to join new colonies that may contain unrelated individuals. This leads to frequent behavioural interactions among females that may be related or unrelated, and familiar or unfamiliar. We used observation nests and microsatellite loci to assess the influence of familiarity and relatedness on behavioural interactions during the early phase of colony development, when females establish reproductive queues prior to brood production. Females were more likely to feed and were less aggressive to familiar rather than related nestmates, regardless of their relatedness. This suggests that eastern carpenter bees primarily use learned cues to discriminate among nestmates. Interactions with nestmates were also context-dependent, as females returning to the nest without food were the recipients of more aggression than those returning with food. If spring dispersal leads to reduced relatedness in *X. virginica* colonies, then nestmate recognition based on familiarity would be an important factor in maintaining group cohesion.

1. Introduction

Animals that live in social groups must frequently decide whether the conspecifics they encounter are part of their established group or are outsiders. Failure to discriminate against non-members may result in the depletion of food or nesting resources (Boff et al., 2015), increased parasitism (Kreuter et al., 2012), the killing of immature or juvenile offspring, and even superseding of dominant individuals (Hogendoorn, 1996; Hogendoorn and Velthuis, 1995), outcomes that can decrease the fitness of the individuals in the group. In contrast, cooperation among group members can optimize their fitness by increasing the efficiency of the colony and offspring survival, and by decreasing parasitism (Clutton-Brock, 2002).

Recognition mediates how individuals make decisions when encountering conspecifics. Two possible types of recognition are the ability to recognize kin and the ability to recognize conspecifics based on cues learned from prior association (Breed, 2014). Individual or nestmate recognition (based on learned rather than shared kinship

cues) occurs when a cue-receiver behaves differently towards familiar or unfamiliar cue-bearers, following a period of contact or a series of interactions (Dale et al., 2001; Sherman et al., 1997). Kin recognition occurs when a cue-receiver behaves differently towards genetically related versus unrelated cue-bearers (Sherman et al., 1997). The cue-receiver must be able to recognize genetic traits identical by descent in the cue-bearer, even without previous contact or interactions.

In social insects, group members typically live together in a shared nest, and related females cooperate in food acquisition, nest maintenance, and rearing of offspring (Michener, 1974). Examples of nestmate recognition are pervasive in social insects, including obligately eusocial wasps (Gamboa et al., 1986a, 1986b), primitively eusocial sweat bees (Soro et al., 2011), ants (Errard, 1994; Rosset et al., 2007), and facultatively social carpenter bees (Peso and Richards, 2010a). Even non-social bees can be capable of nestmate recognition (Flores-Prado et al., 2008). In most cases, cuticular hydrocarbon profiles are used to distinguish nestmates from non-nestmates (Gamboa et al., 1986a; Nunes et al., 2011; Van Zweden et al., 2010), but visual cues

* Corresponding author. Current address: Department of Biological Sciences, University of Calgary, 2500 University Drive NW, Calgary, Alberta, Canada.
E-mail addresses: jvickruck@gmail.com (J.L. Vickruck), mrichards@brocku.ca (M.H. Richards).

have been implicated in individual recognition in *Polistes fuscatus* wasps (Tibbetts, 2002).

In contrast to the widespread evidence for nestmate recognition, convincing evidence for kin recognition in social insects is rare (Breed, 2014). Initial evidence for kin recognition came from the eusocial sweat bee *LasioGLOSSUM zephyrum*, in which workers can discriminate among conspecifics of varying degrees of relatedness without previous contact (Greenberg, 1988, 1979). Very recently, it was found that gregarious cockroaches can discriminate kin based on cuticular hydrocarbons (Lihoreau et al., 2016). Kin recognition is more difficult to detect than previously thought, because it is now known that in many species, colonies contain significant numbers of unrelated individuals (Abrams and Eickwort, 1981; Breed, 2014; Kukuk et al., 2005; Leadbeater et al., 2010). This insight invalidates any assumptions that behavioural discrimination between nestmates and non-nestmates is equivalent to discrimination between kin and non-kin. It has also been demonstrated that in nests which contain multiple matriline or patriline kin discrimination may break down (Ratnieks et al., 2006).

A powerful way to address questions surrounding whether an organism uses nestmate or kin recognition is to test both simultaneously in the same species (Downs and Ratnieks, 1999; Hain et al., 2016; Lihoreau et al., 2007). One explanation is that even in species capable of kin recognition, recognition behaviour may be modified by learning. For instance, in *L. zephyrum*, workers use both kin (Greenberg, 1988) and nestmate recognition (Buckle and Greenberg, 1981) when interacting with nestmates. To fully differentiate between kin and nestmate recognition, it is also necessary to compare recognition in behavioural contexts in which there are definite fitness consequences of discrimination. This is because animals may recognize each other as either kin or nestmates but express discriminatory behaviour only in contexts where there is an advantage to doing so. In social insects, discrimination is expected when nestmates help each other, for instance, by guarding nest entrances from intruders or by feeding nestmates. Predictions about how same-sex nestmates should behave towards one another are based on the underlying assumptions that social insect colonies are composed mainly of kin, that increased cooperation promotes group cohesiveness and the average fitness of group members, and that increased aggression among nestmates decreases fitness (Breed, 2014). When social groups contain a mix of related and unrelated individuals, then both kin and nestmate recognition could operate, and behavioural interactions could be influenced by the relative strengths of kin and nestmate recognition cues. However, discriminatory behaviour can be used to distinguish kin recognition from nestmate recognition based on familiarity. If recognition is based exclusively on cues that relay information about genes shared by descent, then previous experience should not influence behavioural interactions; cooperation should be more frequent among related individuals and aggression should be more frequent among unrelated individuals. Similarly, if recognition is based exclusively on cues that are learned, cooperation should be more frequent between familiar individuals, and aggression should be more frequent between unfamiliar individuals, regardless of genetic relationships. If recognition is based on genetic identity, but can be modified by learning, then we would expect preferential behaviour favouring familiar versus unfamiliar relatives, or favouring familiar relatives over familiar nonrelatives.

An ideal model for simultaneously examining the effects of familiarity and kinship cues on recognition is the eastern carpenter bee, *Xylocopa virginica*, which breeds in colonies that contain both relatives and non-relatives. Siblings overwinter together in their natal nests, but many females disperse to join new colonies during the breeding season (Peso and Richards, 2011; Richards and Course, 2015). As a result, females experience opportunities for two levels of social discrimination, first, between relatives and non-relatives, and second, between natal nestmates they have associated with since the previous summer, and

recent nestmates that have just joined a colony. In a previous study, Peso and Richards (2010) found that both females and males that had spent the previous night in the same nest were more tolerant and less aggressive to each other than pairs of bees from different nests. Together with evidence for frequent relocation of females to new colonies (Peso and Richards 2011) and behavioural evidence for tolerance among nestmates (Vickruck 2017), this suggests that females rapidly learn the identities of new nestmates. However, the ability to learn the identities of new nestmates does not preclude kin recognition, because natal nestmates might be kin. Peso and Richards (2010) did not know which bees were related and did not address the issue of which cues bees used to identify each other. Thus, it remains an open question whether kinship might influence recognition in eastern carpenter bees or whether recognition is based mainly on familiarity.

In this study, we investigate whether nestmate recognition in eastern carpenter bees is influenced by genetic cues that would indicate kin recognition, or is based solely on learned cues and familiarity. Our approach was to examine recognition behaviour during the nestmate provisioning phase of colony development in early spring, prior to egg-laying. During this early phase of the colony cycle, social females feed adult nestmates, suggesting that feeding behaviour is involved in establishing dominance hierarchies and reproductive queues that structure reproductive skew during the brood provisioning phase of the colony cycle (Richards and Course, 2015). As feeding of adult nestmates exemplifies cooperation among group members and aggression between nestmates exemplifies conflict, behavioural interactions during the nestmate provisioning phase provide an opportunity to observe how females naturally interact with conspecifics representing all possible combinations of relatedness and familiarity. This allowed us to investigate the extent to which *X. virginica* females use kin recognition, nestmate recognition based on familiarity, or both in interactions among nestmates. We predicted that if females exclusively use kin recognition to discriminate among individuals they encounter in their own nests, cooperative behaviour should be more frequent and aggression should be less frequent among related than unrelated individuals. Conversely, if recognition is based on familiarity, cooperation should be more frequent and aggression less frequent among familiar than unfamiliar individuals. If both kin and nestmate recognition are used, then related, familiar bees should be the most cooperative and least aggressive, while unrelated, unfamiliar bees should be the least cooperative and most aggressive.

2. Methods

2.1. Seasonal phenology and nesting biology of *Xylocopa virginica*

In southern Ontario, the colony cycle of *X. virginica* begins in April, when adult bees awaken from hibernation. First males and then females emerge from their nests when daytime temperatures first reach 20 °C. For females, a period of nestmate provisioning ensues, during which foragers bring pollen back to the nests to feed to adult nestmates (Richards and Course, 2015). The nestmate provisioning period is followed by the brood provisioning period, which lasts from mid-May until mid-July, after which adult bees mostly remain inside their nests. Brood typically eclose from August to September, but remain inside their natal nests over the winter. Adult bees huddle together at the ends of their burrows throughout the winter (Fig. 1), so natal nestmates spend at least eight months (September–April) in intimate contact.

Female eastern carpenter bees can nest solitarily or socially (Peso and Richards, 2011; Richards and Course, 2015). Social colonies of *X. virginica* are small, typically comprising 2–8 adult females during the brood provisioning phase (Richards, 2011). Prior to emergence from hibernation, nest groups are comprised of natal nestmates produced by one to several mothers. However, with the onset of the nestmate

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