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Research article

Food availability and brood number do not influence intraspecific aggression in Argentine ants

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Summary. Nestmate recognition cues can derive from both environmental and genetic factors, but can also be modulated in response to context-specific cues. Synchronous changes in nestmate recognition systems occur seasonally in some species of ants, however the mechanisms underlying these seasonal changes are often unknown. We studied two mechanisms, relative brood number and food availability, to determine if they generate temporal variation in intraspecific aggression in an introduced population of the Argentine ant, *Linepithema humile*. Using data from previous studies we found that seasonal increases in aggression levels correlate with seasonal increases in brood-to-worker ratios in the field. However, when we manipulated brood-to-worker ratios in paired experimental colonies, we found no direct evidence that relative brood numbers influenced aggression levels. To determine if food availability influenced aggression we conducted a second experiment in which we randomly assigned pairs of experimental colonies to starved or fed treatments and then measured aggression levels weekly for five weeks. We observed no difference in the level of aggression between these two treatment groups indicating that food availability also has no affect on aggression levels between hostile conspecific colonies.

Key words: Argentine ants, brood pheromones, intraspecific aggression, nestmate recognition, resource availability.

Introduction

In social insects, nestmate recognition systems are often well developed and allow colony boundaries to be defended. Most social insects use odour cues based on genetic or environmental labels to distinguish colony members from non-members. These labels help to identify each individual's colony of origin and are used as a recognition template against which individuals can discriminate nestmates from non-nestmates. However, social insect recognition systems can also be dynamic and modulated in response to context-specific cues. For example, the level of aggression displayed by workers towards intruders can depend on the importance of the territory or resource they are defending (Oster and Wilson, 1978; Davies and Houston, 1984; Sakata and Katayama, 2001), the distance an individual is away from the nest (Knaden and Wehner, 2004), experience with the intruding colony (Jutsum et al., 1979; Ydenberg et al., 1988; Gordon, 1989; Dunn and Messier, 1999; Thomas et al., 1999; Langen et al., 2000; Sanada-Morimura et al., 2003), or the time of year (Rosengren et al., 1985; Ichinose, 1991; Suarez et al., 2002).

Seasonal changes in the degree of aggression displayed between conspecific colonies occur in *Formica truncorum* (Rosengren et al., 1985), *Paratrechina flavipes* (Ichinose, 1991) and *Linepithema humile* (Suarez et al., 2002). In these studies, aggression between colony pairs increased in spring and summer. Such variability may be due to seasonal shifts in the way nestmates are recognised. There is a direct association between cuticular hydrocarbon profiles and nestmate recognition in ants (Lahav et al., 1999; Thomas et al., 1999; Boulay et al., 2000; Liang and Silverman, 2000) and recent studies have shown that cuticular hydrocarbon profiles also change seasonally in some ant species (Vander Meer et al., 1989; Provost et al., 1993; Nielsen et al., 1999; Liu et al., 1998, 2001).

Seasonal variation in aggression and cuticular hydrocarbon profiles appear to change in a synchronous manner within colonies (Vander Meer et al., 1989; Provost et al., 1993; Neilsen et al., 1999; Liu et al., 1998, 2001). This synchronous change could be due to extrinsic factors such as variation in diet, temperature or moisture. Although the role of diet in nestmate recognition systems is documented (e.g. Liang and Silverman, 2000; Liang et al., 2001; Lim et al., 2003), less attention has been given to how resource availability affects the level of aggression exhibited between colonies. Food availability certainly influences aspects of a colony's ontogeny. For example, colonies of *L. humile* raised on a high protein diet are more likely to produce reproductive offspring than colonies raised on a low protein diet (Aron et al., 2001). Since the level of protein a colony consumes can influence its reproductive output, colonies in protein-poor environments may be expected to compete more vigorously against aggressive conspecific colonies compared to colonies in protein-rich environments. An increase in resource competition has been linked to higher levels of intraspecific aggression between some ant species (Mabelis, 1984a,b; Sakata and Katayama, 2001; Sorvari and Hakkarainen, 2004).

Intrinsic factors such as reproductive phenology may also induce seasonal changes in aggression levels (Suarez et al., 2002). Within a colony, changes in social structure, such as queen number or presence, can alter the number of conflicts between inhabitants (e.g. Gamboa et al., 1996; Gobin and Ito, 2003). Although there has been conflicting evidence regarding the role of queen pheromones on nestmate recognition cues (e.g. Ichinose, 1991; Boulay et al., 2003; Vander Meer and Alonso, 2002), in *L. humile*, queen pheromones appear to play an insignificant role on aggressive behaviour, at least over the short-term (Caldera and Holway, 2004). Brood, like queens, also emit distinct pheromones in some ant species (Bigley and Vinson, 1975; Zimmerli and Mori, 1993; Mori et al., 1996), however investigations into the influence of brood pheromones on worker behaviour have only recently begun. In bees, brood pheromones stimulate workers to perform particular tasks, including increasing a worker's foraging effort (e.g. Pankiw and Rubink, 2002; Pankiw and Page, 2003; Pankiw 2004). While in some species of slave-making ants, attractiveness of brood could be due to an interspecific brood pheromone (Mori et al., 1996).

In introduced populations of Argentine ants, we found a relationship between seasonal increases in aggression and the brood-to-worker ratio (Fig. 1, data derived from Markin, 1970 and Suarez et al., 2002). Argentine ant colonies follow a seasonal life cycle, with worker brood forming approximately 50% of the colony biomass through the summer months (Markin, 1970), a period when Argentine ant workers exhibit their highest level of aggression (Suarez et al., 2002). During the cooler winter months, brood levels decrease to around 10% of the colony biomass and aggression levels subside. This correlation (Fig. 1) could result from the presence of a brood pheromone that stimulates workers to forage more, thereby increasing competition for food between neighbouring colonies. Alternatively, colonies may simply be hungrier because of the increased demand for food due to higher numbers of larvae. Workers may also be more hostile to aggressive conspecifics because they have a greater investment to protect. In some ant species, the level of aggression displayed by workers towards intruders can depend on the importance of the resource they are defending (Oster and Wilson, 1978; Davies and Houston, 1984; Sakata and Katayama, 2001).

In this study we investigate two cues, relative brood number and food availability, that may instigate temporal changes in intraspecific aggression between supercolonies of the Argentine ant (*Linepithema humile*), a widespread invasive species (Suarez et al., 2001). Introduced populations of *L. humile*, generally form expansive supercolonies in which intraspecific aggression is absent (Newell and Barber, 1913; Passera, 1994; Way et al., 1997; Tsutsui et al., 2000; Giraud et al., 2002). Both environmental (Liang and Silverman, 2000; Liang et al., 2001) and genetic (Tsutsui et al., 2000) factors may contribute to variation in intraspecific aggression. To determine if relative brood number influences aggression level we used paired experimental colonies containing high (1:2) and low (1:50) brood-to-worker ratios. To ascertain if food availability influences aggression, we tested aggression levels between experimental colonies divided into two feeding regimes: starved and fed. Given the lack of intraspecific aggression typical of introduced populations of Argentine ants and its potential role in their success, it is of interest to determine if these factors influence aggression.

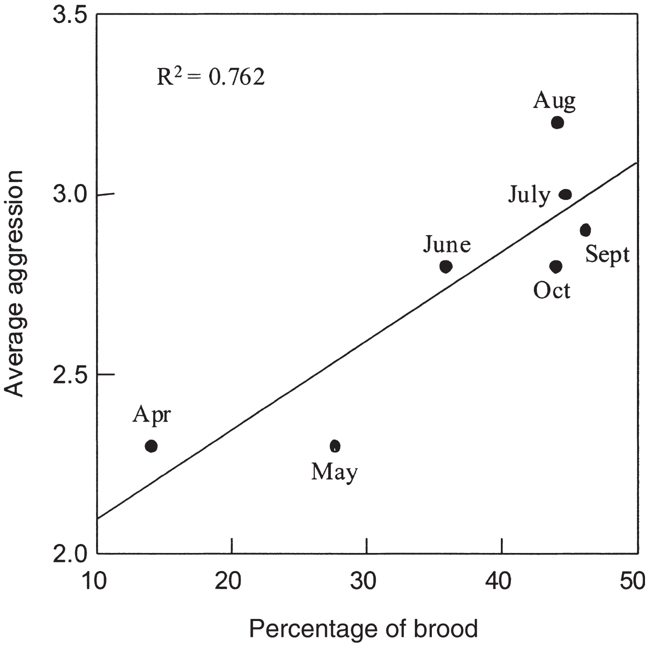

Figure 1. The relationship between average monthly aggression (from Suarez et al., 2002) versus the percentage of brood within colonies (from Markin, 1970) (simple linear regression; $F_{1,5} = 16.00$, $p = 0.01$). The percentage of brood is a measure of the total weight of brood in relation to the total colony mass. We only used months between April and October, as this is the period of most active brood production.

Methods

Nest collection and maintenance

Colonies were collected from five supercolonies: the four supercolonies known to exist in Southern California (Lake Hodges, Sweetwater, Lake Skinner, and the large supercolony) (Suarez et al., 2002) and one additional recently located supercolony (Cottonwood). Within each supercolony except Lake Skinner, we collected colonies from four sites at least 200 m apart from one another. We collected separate nests from each site for both experiments. Within the Lake Skinner supercolony, we collected ants from a single site due to the restricted size of this supercolony.

In the laboratory, colonies were housed in round plastic containers (20 cm diameter) lined with Fluon™. They were provided with nesting chambers consisting of test tubes half filled with water and plugged with cotton wool. Colonies were kept at a constant 25 °C and, unless otherwise stated, were fed sugar water, 10% Casamino acid solution (a form of protein) and scrambled egg, *ad libitum*. We did not feed colonies insects while they were kept in the laboratory, as cuticular hydrocarbons from some insects can be transferred to workers and this can influence nestmate recognition cues (Liang et al., 2001).

Experimental design

We separated nests from each collecting site (except the Lake Skinner collecting site) into two experimental colonies consisting of approximately 1000 workers, 2 queens and 100 pieces of brood unless otherwise stated. The nest collected from Lake Skinner was divided into eight experimental colonies of this size. For each experimental group we paired experimental colonies against all possible combinations of supercolonies. For example, experimental colonies collected from Lake Hodges were paired against experimental colonies from Sweetwater, Cottonwood, Lake Skinner and large supercolony experimental colonies, however not against other experimental colonies collected from Lake Hodges. In addition, experimental colonies were only paired with other experimental colonies from the same treatment group (i.e. high brood experimental colonies against other high brood experimental colonies). This made a total of 10 unique colony pair combinations. Therefore, within each experiment, the two treatment groups contained ten identical pairs of colonies.

Experiment 1: manipulation of brood-to-worker ratios

To determine if the presence of brood increases aggression between conspecific workers, we manipulated brood number within experimental colonies. We divided experimental colonies (containing 1000 workers) from each collecting site into two groups; one with a high brood-to-worker ratio (1:2, approximately 500 brood pieces) and one with a low brood-to-worker ratio (1:50, < 20 brood pieces). The brood consisted of mainly larvae, but also contained eggs and pupae. These treatment levels incorporate an important element of realism because they represent approximate endpoints of natural variation (Markin, 1970). We did not use a category in which brood were completely absent, since this is rarely observed in the field. Experimental colonies were allowed to acclimatise to the social milieu of their colony for a period of two weeks after which we quantified aggression levels between colony pairs using five-on-five behavioural bioassays.

Experiment 2: manipulation of food levels

To determine if food availability influences aggression between conspecific workers we divided experimental colonies into two food treatments: one treatment group was fed a diet of sugar water, 10% Casamino acid solution (protein) and scrambled egg *ad libitum*, colonies in the other treatment had access to water *ad libitum* but were deprived of food. We measured the level of intraspecific aggression between starved and fed colony pairs at five time intervals: one day prior to the food treatments commencing (both treatment groups were at the same satiation level) and one, two, three and four weeks following commencement of the different feeding regimes.

Five-on-five behavioural biossays

We performed five-on-five behavioural bioassays to estimate aggression in both experiments. Five-on-five behavioural biassays provide consistent results when balanced against one-on-one bioassays and colony-level interactions (Roulston et al., 2003). We modified the five-on-five behavioural bioassay used in Roulston et al. (2003) to incorporate timing of aggressive behaviour and level of aggression. Five ants from each collection site were placed in a 10 cm^2 petri dish lined with fluon to prevent the ants from escaping. We scanned behaviour every minute for 10 minutes, classifying each workers behaviour into one of four categories: (1) no interest (workers show no aggressive interest in other workers), (2) mandible gaping, avoidance (the ants touch, and one or both recoils and runs in the opposite direction) or intense antennation (workers show more than a passing interest in each other), (3) aggression (a physical attack by one or both of the workers, including lunging, biting or pulling of legs or antennae), (4) fighting (prolonged aggression, that results in death or severe injury and can include the use of chemicals). Pilot trials showed that once workers were involved in a level-four fight, it would end with one or both individuals being killed or severely injured (see also Tsutsui et al., 2003). Therefore, to avoid any chance of workers from one colony being more competent fighters compared to workers from the opposing colony (see Tsutsui et al., 2003), we removed ants once fighting reached level four. These ants were then categorized as a level four for the time remaining after their removal. Most level four fights involved only two workers.

A single aggression index ranging from 1 (no aggression) to 4 (intense aggression) was calculated from these 10 minute trials. We did this by calculating the proportion of ants involved in each behavioural category at each minute increment. From the proportions we calculated the average for each behaviour category. We then multiplied the average of each behaviour category by the aggression index for that behaviour (1–4), and the sum of these numbers gave the final aggression index. One indicated no aggression throughout the ten scans, four indicated that all ants were fighting at the highest level within the first minute. This aggression index therefore reflects not only the level of aggression, but also how fast workers initiated aggression. Observers were blind to the colony or treatment identity of the ants.

Data were analysed using paired t-tests with the software package SYSTAT 9.0 (Wilkinson, 1998). All errors are standard errors if not otherwise stated.

Results

Manipulation of the brood-to-worker ratio did not affect the level of intraspecific aggression (Fig. 2). Workers from colony pairs containing high brood levels were not more aggressive after two weeks compared to workers from colony pairs in which brood were scarce (mean aggression rating for high brood-to-worker ratio = 1.87 ± 0.18; low brood-to-worker ratio = 1.88 ± 0.18; paired t-test: t = –0.221, d.f. = 9, p = 0.83).

Prior to placement on different food treatments, colony pairs did not differ in the level of aggression exhibited between fed and starved treatments (mean aggression rating for fed colony-fragment pairs = 2.19 ± 0.16; starved colony-fragment pairs = 2.308 ± 0.17; paired t-test: t = –0.716, d.f. = 9, p = 0.492) (Fig. 3). Two weeks following commencement of the different food treatments, aggression between fed and starved experimental colonies still did not differ (mean aggression rating for fed colony-fragment pairs = 2.085 ± 0.126; starved colony-fragment pairs = 2.150 ± 0.163; paired t-test: t = –0.338, d.f. = 9, p = 0.743) (Fig. 3). This qualitative pattern was also observed one, three and four weeks following commencement of the food treatments.

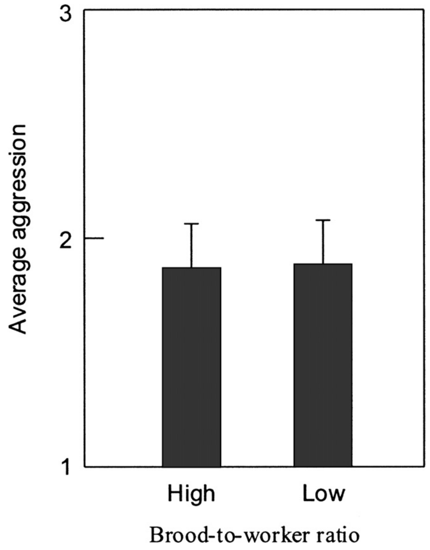

Figure 2. Mean (± SE) level of intraspecific aggression for pairs of experimental colonies containing a high or low brood-to-worker ratio. Each bar represents the mean level of aggression of ten colony pairs. Aggression did not differ between the two brood treatments.

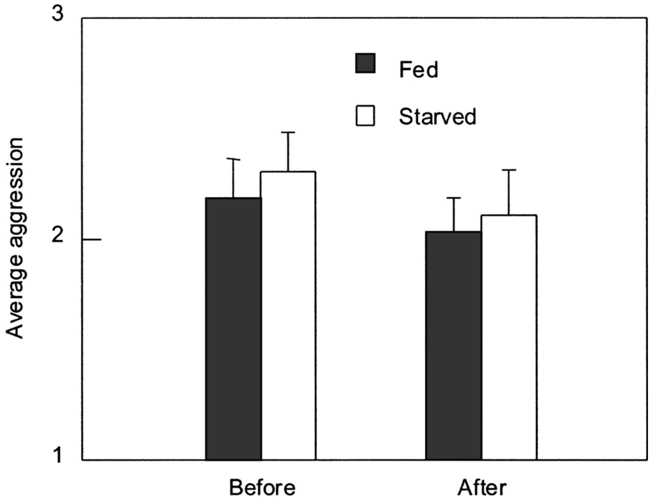

Figure 3. Mean (± SE) level of intraspecific aggression for fed (black bars) and starved (white bars) pairs of experimental colonies at two time intervals; before colonies were placed on the two food regimes and two weeks following the commencement of the food treatments. Each bar represents the mean level of aggression of ten colony pairs. Aggression did not differ between food treatments at either time interval.

Discussion

In this study, we obtained no evidence that short-term shifts in food availability altered intraspecific aggression in Argentine ants. In addition, we found that brood numbers do not affect aggression levels, indicating that any pheromones emitted by *L. humile* brood do not profoundly alter nestmate recognition behaviour. These results suggest that seasonal increases in aggression have their root cause in factors other than those examined here.

It is unlikely that the type of behavioural assay used in this study influenced our results. Although the environmental setting can be an important factor when investigating aggressive behavioural interactions (Sakata and Katayama, 2001; Knaden and Wehner, 2003; Breed, 2003), studies using different bioassay techniques with Argentine ants have yielded similar results (Roulston et al., 2003; Caldera and Holway, 2004). Furthermore, despite our bioassays being undertaken out of the colony environment, they are consistent with previous observations involving colony-colony interactions between these supercolonies (Holway et al., 1998; Holway and Suarez, 2004).

Aggression levels were generally lower in experiment 1 (manipulation of brood-to-worker ratio) relative to experiment 2 (manipulation of food levels). There are a number of possible reasons for this variation. First, experiment 1 was undertaken in May, a period when Argentine ant colonies are generally less aggressive, while experiment 2 was performed in July, when Argentine ant colonies are more aggressive (Suarez et al., 2002) (Fig. 1). Second, different observers contributed to the two experiments. And lastly, aggression levels in Argentine ants exhibit an inherent amount of variation (Suarez et al., 2002).

Our results from the brood manipulation experiment seem consistent with one particular feature of the ecology of *L. humile*. Individual nests that make up colonies of *L. humile* are often ephemeral, and interchange of workers, brood and queens among nests can be high (Newell and Barber, 1913; Markin, 1968, 1970). This within-colony flux of brood and workers may compromise the effectiveness of brood pheromones as a nestmate recognition cue.

Although hunger does not appear to trigger higher levels of aggression, it may indirectly contribute to variable aggression levels. For example, a restricted food supply may elicit an increase in a colony's foraging effort or its level of competition with neighbouring colonies. An increase in nest activity may be responsible for seasonal shifts in aggression levels between conspecific colonies of *P. flavipes* (Ichinose, 1991). We cannot exclude the possibility that starved colonies were supplementing their diets with dead workers, brood or trophic eggs. However, it seems unlikely that this source of food would have sustained a colony at the same satiation level for five weeks, compared to colonies in the treatment with food.

There are a number of alternative factors that could produce the seasonal increase in aggression levels observed by Suarez et al. (2002). For example, temporal changes in within-nest relatedness or changes in local worker density could result from queen turnover and colony contraction and expansion (Suarez et al., 2002). In addition to the production of new workers during the summer months, contraction of colonies into fewer nest sites results in an increase in the local worker density (Markin, 1970). An increase in local worker density may also cause an increase in nest activity, which could influence aggression levels (Ichinose, 1991). The number of queens within a nest may also increase when separate nests coalesce. In some species, multiple-queen colonies can possess weak recognition abilities relative to single-queen colonies (e.g. Morel et al., 1990; Starks et al., 1998). Although presence or absence does not appear to influence aggression levels between *L. humile* colonies over the short-term (Caldera and Holway, 2004), it is possible that over longer periods, the number of queens contributing to the genetic make-up of the colony could influence relatedness between nestmates. Since nestmate recognition in Argentine ants is thought to have a strong genetic component (Tsutsui et al., 2000, 2003), any change in the genetic structure of a colony could potentially alter aggression levels with other conspecific colonies. The role of extrinsic environmental factors such as temporal variations in temperature, moisture or changes in circadian rhythms remains to be determined.

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