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Opportunistic discrimination of alien eggs by social wasps (*Polistes biglumis*, Hymenoptera Vespidae): a defense against social parasitism?

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Abstract Foundresses of the social wasp *Polistes biglumis* were tested to see whether they were able to recognize alien eggs experimentally introduced into their own nests. Foundresses removed alien conspecific reproductive-destined eggs while they accepted worker-destined eggs. The results indicate that social wasps discriminate among eggs and that they discriminate against alien eggs destined to produce unrelated reproductives. *P. biglumis* is a strictly solitary founding species, with no reproductive competition within colonies; thus, brood discrimination abilities could have evolved as a counteradaptation against intra- and inter-specific brood parasitism.

Key words Brood recognition · Egg discrimination · Social parasitism · Social wasps · *Polistes*

Introduction

Individuals of some species can discriminate between the eggs they lay and the eggs others lay: researchers observe the removal of foreign eggs from the nest. This behavior has been reported in birds (reviewed by Rothstein and Robinson 1998) and in many species of social insects (reviewed by Crespi 1992). Natural selection may have favored egg-discriminating abilities for various reasons.

In birds, where egg removal has been explicitly tested (e.g., Davies and Brooke 1989a, 1989b; Moksnes et al. 1991), discriminating species are often host species of obligate brood parasites, such as cuckoos: hosts can discriminate between the eggs they lay and those laid by parasites in their nests. European cuckoos lay eggs which mimic those of the hosts, so that hosts must detect subtle visual differences to recognize parasite eggs. Usual-

ly, in host populations with a low rate of brood parasitism, hosts show greater acceptance of unlike eggs (reviewed by Davies and Brooke 1998), and thus recognition (and ejection) of parasite eggs is considered a defense mechanism against brood parasitism evolved by hosts in an arms race with brood parasites (e.g., Davies et al. 1989; Rothstein and Robinson 1998 for a review).

In social insects, where reproduction is monopolized by a small proportion of individuals within a colony, selective removal of eggs is common (Crespi 1992). In general, it has been reported in two different contexts: as performed by workers or by reproductives to promote, respectively, their inclusive or their direct fitness. In some species such as the honeybee, workers constantly screen eggs and remove worker-laid eggs (worker policing; Ratnieks and Visscher 1989; Ratnieks 1993, 1995; Visscher 1996). Egg cannibalism by workers has also been reported in ants (e.g., Peeters and Tsuji 1993; Bourke 1994). In these cases, workers discriminate between queen-laid and worker-laid eggs: they care for the former and eat the latter. In other insect societies, where several potential egg-laying queens cohabit in the same colony at least temporarily, the dominant fertile female detects and removes eggs laid by subordinate (or ex-dominant) females (e.g., in ants, Bourke 1991, 1994; in wasps, Gervet 1964; West-Eberhard 1969; Field and Foster 1999). Therefore, the ability of social insects to discriminate eggs is usually linked to reproductive competition within a colony. As far as we know, the possibility that egg discrimination by social insects might have evolved as a counteradaptation to brood parasites, or social parasites (as brood parasites are more often called in social insects) has never been tested. This is reasonable, since selective oophagy has been described in multiple-queen species, so there seems to be a link between reproductive competition and differential eating of eggs. Moreover, in many social insects, social parasites chase out the host queen when they take over the host colony, avoiding the possibility that she eats their eggs (Wilson 1971; Fisher 1983; Cervo and Dani 1996). However, in ants, Bourke (1994) documented that queens discriminate eggs and

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suggested that they might have evolved this ability as a defense against conspecific and obligate social parasites. Gamboa (1996) speculated that the ability to distinguish brood and to characterize them with a chemical signature could be a way to defend against inter- and intra-specific brood parasites.

In *Polistes* wasps, differential oophagy has been observed in multiple-foundress colonies (Gervet 1964; West-Eberhard 1969): dominant females eat eggs laid by subordinate fertile females.

However, oophagy is also performed by queens in single-queen colonies of *Polistes* wasps, where there is no direct reproductive competition between foundresses because each queen establishes a nest on her own. Indeed, in species where colonies are founded by a single queen, queens do eat foreign eggs when they usurp or adopt conspecific colonies and behave as social parasites: usurpers may kill or evict the original foundress and eliminate eggs, although they do care for most developed brood (reviewed in Cervo and Dani 1996, but also recently Starks 1998).

When a female wasp is able to detect and remove an egg laid in her nest by nestmates, the cue for their recognition is presumably some (chemical) signature. The signature could be deposited on eggs or on the cells which contain them (i.e., on the nest paper around the egg). For *Polistes* wasps, Downing (1991) provided evidence that Dufour's gland may be involved in the discrimination between self and alien-laid eggs in multiple-foundress colonies. In contrast, queens in haplometrotic species, which do not experience any reproductive competition, should not have been selected to mark eggs.

Indeed, in all species of *Polistes*, the ability to distinguish between own and alien eggs has been inferred by behavioral observations, but no experiment has ever been performed to test whether queens discriminate between their own and others' eggs. *Polistes* wasps learn their colony odor from the nest paper and rely on the learned odor for recognition processes: when they eat foreign eggs, do they really recognize them? And do they recognize them by cues borne on eggs, or by cues coming from the paper around the egg, or from the comb which contains the egg? To answer these questions, we transplanted eggs between nests and observed the behavior of foundresses offered a choice between their own eggs and those of other queens. The experiment was performed in a species (*Polistes biglumis*) where there is neither reproductive competition among foundresses nor between foundresses and workers, since colonies are controlled by single queens and a short colony cycle prevents workers from laying (Lorenzi and Turillazzi 1986). Apparently, therefore, this is one of the species of *Polistes* wasps in which queens might not be selected to detect eggs laid by others: the foundress, alone on her nest for half the colony cycle, has no reproductive competitors. However, the population studied has a very high rate of social parasitism by conspecific females (Lorenzi and Cervo 1995) and by *P. atrimandibularis*, an obligate social parasite (Cervo et al. 1990). *P. atrimandibularis* females

enter a host nest about 1 month after its foundation, subdue the only resident foundress and begin egg-laying themselves. A parasite queen and her host foundress live together on the host nest for about 1 month, after which, host workers begin to emerge (Lorenzi et al. 1992).

In birds, brood parasitism is thought to have favored in the hosts the ability to recognize parasite eggs. Similarly, in our wasp population, inter- and intra-specific social parasitism could have promoted the selection of egg recognition ability. Thus, we discuss the possibility that, if it exists, an ability to distinguish between own and alien eggs could have evolved as a counteradaptation to brood parasitism.

Methods

P. biglumis (*P. biglumis bimaculatus* of authors preceding Carpenter 1996) in Italy is a mountain species. A single foundress builds her nest at the beginning of June, and remains the only adult on the colony until the end of July, when workers begin to emerge; the colonial cycle ends by mid-September (Lorenzi and Turillazzi 1986). In our experiment, we transplanted eggs of *P. biglumis* wasps into a foreign conspecific nest or, as controls, back into their original nest. We evaluated how many eggs were tolerated (and how many were removed) by the nest foundress of each colony. The experiments were performed during the pre-worker phase, when the foundresses were the only adult on each colony.

In summer 1997 and 1998, we collected 35 colonies of *P. biglumis*. Collections took place on different dates from mid-June through July (i.e., when egg-laying activity is at its peak). All colonies were brought to the laboratory, and foundresses were temporarily moved from their nests to prepare the nests for the experiment. Nests were censused for the number and position of eggs, larvae, and pupae; then all eggs were gently removed from their cells (with the exception of 14 eggs, see below). Colonies were in the pre-emergence phase of the colony cycle.

P. biglumis eggs

The experiment consisted of 299 *P. biglumis* egg exchanges: each egg was extracted from its cell with a thin needle and was either introduced into a cell in a foreign nest (experimental or foreign eggs, $n=170$), or reintroduced into its original cell (control or own eggs, $n=129$). *Polistes* eggs are glued on walls at the bottom of nest cells, so egg removal is difficult. Many eggs were obviously damaged by our manipulation and will not appear among the values given in the results below. Egg exchanges were performed between unrelated colonies (i.e., colonies that had been found at least 100 m from each other) to avoid possible kinship recognition between foundresses and foreign brood. When replacing each egg, we placed it in one of the cells that originally contained an egg; within a cell, the egg was placed exactly in the position occupied by the original egg (there was no need to use glue, as eggs are sticky enough to attach to the nest paper). The needle and any tool used in the manipulation were washed in pentane after each egg manipulation to avoid odor contamination of eggs or nests.

As a further control for egg survival in the laboratory, 14 additional eggs (1 in each of 14 of the collected nests) were left in their cells without manipulation (non-manipulated eggs).

Screening for egg survival

Immediately after egg exchanges, each nest was placed in a plastic box (approx. 10×15×12 cm) along with its original foundress: the experiment had been planned so that each foundress would find both her own and alien eggs. However, 10 of 35 foundresses were

only tested with own *or* with alien eggs, due to egg damage during manipulation.

Colonies were supplied daily with honey, water and *Tenebrio molitor* larvae and kept with artificial lightening at 12/12 h light/dark.

Although the egg stage lasts about 2 weeks (Wheeler and Wheeler 1979), checks were made early after the manipulation to evaluate the immediate reaction of foundresses to the presence of foreign eggs. Between 48–72 h after manipulation, we checked to see which eggs were present (=tolerated or accepted eggs). When present, an egg was considered dead when its color had changed to orange-yellow and it was dehydrated, while an egg was considered alive when its original pale-yellow color and smooth surface had been preserved. When an egg had disappeared, it had presumably been eaten by the foundress and will be referred to as an eliminated egg. No eggs were found at the bottom of cages.

When evaluating data, eggs were distinguished as worker-destined and reproductive-destined eggs on the basis of the period when they had been laid by the foundresses: eggs were considered destined to produce workers when they had been laid before 7 July 1997 or 29 June 1998 ($n=122$), and reproductives when they were laid after 15 July 1997 or 17 July 1998 ($n=177$) (according to Reeve and Nonacs 1992, distinguishing egg destiny on the basis of the period when they are laid).

The destiny of *dead* eggs was evaluated again by checking their presence or absence 8 days after manipulation.

The stage of development of brood inside the colony was used to classify colony development: colonies which had at least one larva will be referred to as medium-developed colonies; if they had at least one pupa, they will be referred to as highly developed colonies.

Statistical analyses

Data from 1997 and 1998 collections showed no significant differences (test for heterogeneity, $\chi^2=1.172$, $df=1$, n.s. $P>0.05$) and are treated together in the results. To avoid pseudoreplications, each colony contributed a single datum (e.g., proportion of own or proportion of alien eggs accepted by each foundress with respect to the total number of own or alien eggs introduced into her nest). We used non-parametric statistical tests following Siegel and Castellan (1988); all tests are one-tailed (because queens are unlikely to prefer eating their own eggs).

Results

Of 29 foundresses confronted with eggs they laid and eggs laid by other queens, 69% preferentially ate other queens' eggs rather than their own. Thus foundresses of *P. biglumis* were more tolerant toward their own eggs than toward alien eggs; differences between the two groups were highly significant (Wilcoxon rank-sign test, number of changes=25, $T^+=267$, $z=2.85$, $P=0.0022$).

However, foundresses proved to behave differently when confronted with worker-destined or with reproductive-destined eggs. They did not distinguish between worker-destined eggs laid by themselves or by other foundresses and accepted on average $75\pm 25\%$ (mean \pm SD) of those they laid themselves and $53\pm 32\%$ of those laid by other queens (of a total of 68 alien and 54 own eggs in 12 queenright nests; Wilcoxon test, number of changes=11, $T^+=51.5$, $P=0.0615$, n.s.). In contrast, they were selective when confronted with reproductive-destined eggs: they accepted on average $71\pm 29\%$ of those they laid themselves but only $41\pm 37\%$ of those laid by other

queens (from a total of 102 alien and 75 own eggs in 16 queenright colonies; Wilcoxon test, number of changes=14, $T^+=90$, $P=0.0083$). Thus foundresses were less tolerant of alien eggs when they were reproductive destined.

Foundresses could switch to a higher level of egg discrimination following colony development: the stage of the immature brood inside the colony could have been the signal for tuning egg selectivity. To test this, we examined differences in egg discrimination between colonies that had been collected in the same period but were at different stages of brood development. Foundresses in medium- or in highly-developed colonies showed no significant variation in the acceptance of own and alien eggs (Wilcoxon-Mann-Whitney *U*-test, $z=-0.83$, $n=13, 15$, $P>0.05$). Thus, although egg discrimination abilities vary during the season, our data do not support the hypothesis that foundresses change their selectivity based on the development of immature brood.

Eight days after egg transfer, we checked for the presence or absence of those eggs which, although not eaten in the first check, had been noted as probably dead from their appearance. Discrimination of alien eggs had continued after the first check: after 8 days more own-dead than foreign-dead eggs remained in the nests (sign test, number of changes=8, $P=0.035$).

Laboratory mortality, for non-manipulated eggs, was of course significantly lower than that for manipulated eggs: of 14 untouched eggs, 11 were cared for, 1 died, and 2 were eliminated. These data highlight the effect of our experimental manipulation, but also show that (at least in the laboratory) not all eggs are viable or considered worthy of further development by their mothers.

Discussion

Our egg-switching experiments demonstrate that *P. biglumis* females are able to discriminate between their own and foreign reproductive-destined eggs, and that they eliminate from their combs those that they did not lay. The ability to discriminate brood had been suggested in *Polistes* wasps based on circumstantial data, but it was unclear whether wasps recognize brood directly (Gamboa 1996). In past observations and experiments involving brood recognition, foundresses were presented with immature alien brood inside alien combs (e.g., Lorenzi and Cervo 1992 for *P. biglumis*) and may have recognized foreign brood indirectly (by recognition of chemical cues present in foreign comb) *or* directly (through chemical cues present on the eggs). Our results here demonstrate that *P. biglumis* wasps can discriminate their own from unrelated brood through cues which are located on the eggs themselves. Foundresses ate other queens' eggs which we introduced into their nests. Interestingly, however, discrimination against eggs was exhibited only toward those destined to produce reproductives. Foundresses tended, in contrast, to care for unrelated eggs destined to produce workers. These varying responses by

foundresses likely result from different fitness pay-offs for discrimination of the two egg types. When confronted with unrelated eggs, although foundresses initially pay costs in caring for worker-destined eggs, these are essentially regained by the help received from mature workers once these emerge from the cells. In contrast, care for unrelated reproductive-destined eggs is costly, as there are no immediate or future fitness returns. Eggs which are destined to produce fertile offspring are laid after those destined to produce workers; indeed, foundresses are more selective toward eggs in an advanced stage of the colony cycle, that is, when reproductive-destined eggs are laid. We do not know whether a female can distinguish the odor of worker- from that of reproductive-destined eggs. Alternatively, tolerance of alien odors might decrease as the colony cycle proceeds (tolerance towards foreign adults is known to decrease as well; Gamboa et al. 1991). Our data exclude the possibility that the level of brood development inside the nest is a signal for such a modification.

Chemicals mediate recognition processes in the social insects. The insect cuticle is covered by a thin layer of waxes, of which the main constituents are a series of long-chain hydrocarbons (Lockey 1988; de Renobales et al. 1991). Besides their primary function of regulating water loss, in social insects, a large body of evidence suggests these waxes are also important in mediating the recognition of nestmates, sexual mates, and caste (Howard 1993; Gamboa 1996). Similarly, in *Polistes*, hydrocarbons covering the wasp cuticle and nest paper have been shown to be sources of colonial recognition pheromones (Singer and Espelie 1992; Lorenzi et al. 1997), and the brood is likely a further source. Our results indicate that reproductive-destined eggs at least are likely to express a distinctive chemical signature (eggs could be "chemically marked" by foundresses when they are laid; Downing 1991; Dani 1995). Evidence from other social insects suggest that this may be a general phenomenon. In the queenless ponerine ant *Dinoponera quadricaps*, mated reproductive workers (gamergates) lay eggs that contain significantly higher levels of a single hydrocarbon on their surface (Monnin and Peeters 1997). This allows gamergates to eat selectively any eggs laid by subordinate individuals. In the honeybee, queens lay eggs marked by substances from Dufour's gland: worker-laid eggs lack these substances and are therefore eaten (Ratnieks 1995).

Whether *P. biglumis* foundresses are able to recognize eggs produced by their social parasite *P. atrimandibularis* is not known. Four queens used in the present experiment were also tested to see whether they eliminated *P. atrimandibularis* eggs introduced in their nests (five eggs per nest). Although our sample size was too small for statistical analysis, host foundresses did destroy a percentage of parasite eggs (60.4%), and one of them was very effective in her selection. Further experiments are needed to document whether hosts are able to recognize parasite eggs. However, as *P. biglumis* foundresses are able to detect conspecific queens' eggs, they might

be able to detect those of a different species (*P. atrimandibularis*) even more easily, unless parasite eggs mimic perfectly the odor of the host queen's eggs.

Egg recognition and egg marking with distinctive traits are considered costly behaviors in birds (Davies and Brooke 1998). For example, individuals rejecting unlike eggs may make recognition mistakes and reject their own eggs (Davies and Brooke 1988; Lotem et al. 1995). Such behaviors are also expected to be costly in the social insects. In our experiment, foundresses destroyed about 25% of their own eggs. The possibility that this is an artifact of the experimental manipulation cannot be ruled out; however, a small percentage (about 14%) of eggs which were not subjected to any experimental manipulation were eaten by foundresses. This could be caused by recognition mistakes.

If egg recognition and discrimination are costly, why then do *P. biglumis* wasps exhibit such behaviors? Colonies in *P. biglumis* are always initiated by a single foundress and thus there is never competition over egg production. However, the studied population experiences high rates of social parasitism. Under these conditions, the evolution of both distinctive signature traits in eggs and of discrimination abilities in female foundresses may be responses to the pressure of social parasitism.

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