Context-dependent nestmate discrimination in the paper wasp, *Polistes dominulus*: a critical test of the optimal acceptance threshold model

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ABSTRACT

We present evidence that nestmate discrimination in the eusocial paper wasp, *Polistes dominulus*, is context dependent. We compared aggression levels between nestmates and non-nestmates in dyads consisting of a pair of either nestmates or non-nestmates, and triads consisting of either three nestmates, three non-nestmates, or two nestmates and a non-nestmate. In 130 of the 237 total trials, a nest fragment (containing both brood and eggs) from the nest of some, all or none of the interactants was placed into the interaction arena. *Polistes dominulus* workers recognized and discriminated nestmates from non-nestmates, familiar from unfamiliar nest material and neighbours from non-neighbours. These findings suggest that nestmate and neighbour discrimination are context dependent: discrimination occurs when either the presence of a nestmate or a familiar nest fragment indicate the proximity of the colony. The context-dependent variation in aggression levels is best described by multiple, context-dependent shifts in an acceptance threshold. Thus this study provides the most extensive, critical support yet obtained for Reeve's (1989, *American Naturalist*, **133,** 407–435) optimal acceptance threshold model.

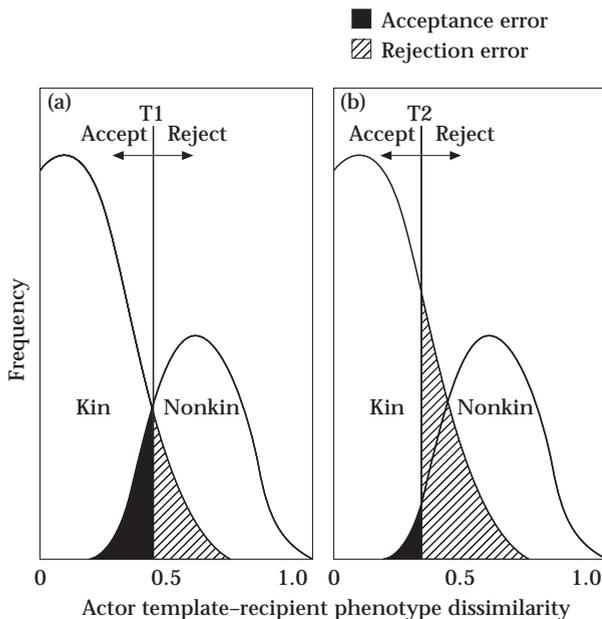© *1998 The Association for the Study of Animal Behaviour*

Natural selection will favour an altruistic behaviour when the fitness cost to the actor is lower than the fitness benefit to the recipient, after the benefit is devalued by the level of relatedness between the actor and recipient (Hamilton 1964a, b). Thus, an organism can maximize the genetic reward for altruism by directing altruism at the most closely related kin (Holmes & Sherman 1983). Indeed, kin discrimination has been well documented in many animals (reviewed in Fletcher & Michener 1987; Blaustein et al. 1988; Hepper 1991; Gamboa 1996).

Kin discrimination, the differential treatment of kin (Holmes & Sherman 1983), can be described in terms of production, perception and action components (Holmes & Sherman 1983; Gamboa et al. 1986; Reeve 1989; Sherman et al. 1997). The production component refers to the nature and manufacture or acquisition of recognition cues that correlate with genetic relatedness, whereas the perception component refers to the mechanism of sensing, processing and matching the recognition cues

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to the perceiver's recognition template (i.e. the mechanism of recognizing kin). Finally, the action component refers to action initiated based on the degree of match between the cue and the template (i.e. the behavioural discrimination between kin and nonkin). Note that recognition does not always lead to discrimination (Reeve 1989).

Reeve (1989) developed the optimal acceptance threshold model to predict the plasticity of the action component. Reeve's model assumes that that there is variability in recognition cues and that individuals develop a recognition template to evaluate how closely these cues resemble those of a desirable conspecific (e.g. kin). Because an invader's cues will seldom exactly match the observer's template, some degree of dissimilarity between the recognition cues and template will normally exist. Among kin, a certain amount of dissimilarity is expected in situations where cues are likely to change over time (e.g. environmental cues) and where kin groups have a nonclonal genetic structure, especially when individuals from multiple genetic lines coexist (e.g. social insects). However, the degree of dissimilarity between interacting kin should generally be lower than that between nonkin (Fig. 1). Errors in recognition (e.g.

■ Acceptance error
▨ Rejection error

Figure 1. Frequency distributions of dissimilarity between the actor's recognition template and the invader's recognition cues; (a) and (b) represent different contexts. In context (b) the cost of accepting a nonkin is greater than in context (a). The cost of rejecting kin is assumed to be equal between contexts. T1 and T2 are the optimal thresholds above which individuals are rejected (aggressed against) and below which individuals are accepted (treated tolerantly). Note that as the cost of accepting nonkin increases, the threshold is predicted to become more restrictive and as a result more kin (and nonkin) will be rejected. Adapted from Reeve (1989).

acceptance and rejection errors) will occur in cases where degrees of dissimilarity overlap between groups (Reeve 1989).

In his model, Reeve (1989) defined the acceptance threshold as the level of dissimilarity between a recognition template and recognition cues below which conspecifics are accepted and above which they are rejected. Reeve also argued that fitness-maximizing thresholds should vary with factors such as frequency of contact with kin or nonkin, and fitness consequences of accepting or rejecting each. Specifically, the acceptance threshold should optimally balance the fitness costs of acceptance and rejection errors. As the fitness cost of accepting nonkin increases, the probability of rejecting both nonkin and kin should increase; that is, the threshold should become more restrictive (Fig. 1). Thus, Reeve's model provides a theory of the context-dependency of kin discrimination.

The optimal acceptance threshold model applies to a wide range of recognition systems, not merely kin recognition (Sherman et al. 1997). For example, female fiddler crabs, *Uca annulipes*, prefer large males early in the mating period but the preference vanishes at the end of the mating period (Backwell & Passmore 1996). This preference switch suggests that females evaluate male quality against a mate template, where high-quality males closely match the template and thus are considered desirable. Time constraints on the female's ability to produce viable

offspring determine the costs and benefits of accepting or rejecting a male of a given quality. Using the framework of the optimal acceptance model, female fiddler crabs display a more restrictive mate choice threshold early in the season and thus choose high-quality males, and a less restrictive threshold when time is limited.

Reed warblers, *Acrocephalus scirpaceus*, and meadow pipits, *Anthus pratensis*, display threshold responses with respect to brood parasitism by the cuckoo (Moksnes et al. 1993; Davies et al. 1996). Meadow pipits and reed warblers' discrimination thresholds become more restrictive when either adult cuckoos or parasitic eggs are observed and are most likely to discriminate when both cues are present (Moksnes et al. 1993; Davies et al. 1996). Similarly, enhanced aggression between nonkin in the marbled salamander, *Ambystoma opacum*, is observed only when the different contexts of kinship, food availability and body size are analysed simultaneously (Hokit et al. 1996). Cannibalistic spadefoot toad, *Scaphiopus bombifrons*, tadpoles eat nonkin when not deprived of food, and both kin and nonkin when deprived of food (Pfennig et al. 1993). These context shifts can all be explained by the optimal acceptance threshold model. However, few studies have examined the optimal acceptance threshold model explicitly and, as yet, no critical test of the model has been published.

In our 2-year study we focused on context-dependent changes in the action component by examining nestmate discrimination in the eusocial paper wasp, *Polistes dominulus*. When examining kin discrimination in social insects, the term 'nestmate' is used in preference of 'kin' because the degree of genetic similarity between colony members is sometimes unknown. However, because nestmates in *Polistes* are usually more closely related than are non-nestmates (Strassmann 1996), the terms nestmates and kin are used interchangeably for this study.

Nestmate discrimination is perhaps best understood in *Polistes* wasps, and virtually all *Polistes* wasps examined display nestmate discrimination (reviewed in Gamboa 1996). Pratte (1982), however, claimed to find no evidence of the behaviour in *P. dominulus*, which he had incorrectly identified as *P. gallicus* (Reeve 1991). Pratte (1982) may have assigned individuals to kin and nonkin groups inaccurately (Gamboa et al. 1986). Alternatively, the testing context used may account for Pratte's inability to observe nestmate discrimination in *P. dominulus*: nestmate discrimination in the wasps *Polistes fuscatus*, *Ropalidia marginata* and *Polistes exclamans* varies with factors such as proximity to the nest and whether or not the intruder is a neighbour (Pfennig 1990; Gamboa et al. 1991; Venkataraman & Gadagkar 1992).

Optimal discrimination theory predicts that discrimination against non-nestmates in *P. dominulus* depends on the social context. To test this, we compared aggression and tolerance between nestmates and non-nestmates in three different contexts: (1) in dyads consisting of a pair of nestmates; (2) in dyads consisting of a pair of non-nestmates; and (3) in triads consisting of two nestmates and a non-nestmate. In addition, we compared aggression between neighbour non-nestmates and non-neighbour non-nestmates.

We found discrimination against non-nestmates in triads but not in dyads. We tested two hypotheses to explain this shift in recognition context. The nest indicator hypothesis proposes that the presence of a nestmate suggests proximity to the nest, thus indicating a fitness payoff for active defence. The cost minimizer hypothesis suggests that nestmates will share the cost of aggressively repelling a non-nestmate but will not absorb the cost of aggression singly. To tease these two hypotheses apart, we added to the basic triad and dyad design a nest fragment (containing both brood and eggs) from the nest of some, all, or none of the interactants. As such, we examined nest fragment recognition, nest fragment defence and discrimination in the absence of a nestmate.

Finally, we tested two hypotheses that describe the behaviour of *P. dominulus* once the animal is in a discrimination context. Since no recognition system is perfect, errors in discrimination are expected (Reeve 1989; Sherman et al. 1997). Our hypotheses differ in the expected frequency of discrimination errors (i.e. acceptance and rejection errors). The fixed error hypothesis suggests that a baseline frequency of discrimination errors will be observed, but that this frequency is not context-dependent. Alternatively, the optimal acceptance threshold hypothesis suggests that discrimination errors are a function of the relative costs of acceptance and rejection errors in a given context, and are thus predicted to vary with different contexts. To test these hypotheses, we examined aggression between nestmates. The fixed error hypothesis predicts that aggression between nestmates will remain constant across different contexts, whereas the optimal acceptance threshold model predicts that aggression between nestmates will increase as the acceptance threshold becomes more restrictive (Reeve 1989). By examining both nestmates and non-nestmates in different contexts, we also examined the plasticity of acceptance thresholds in *P. dominulus.*

METHODS

Methods 1995

We observed *P. dominulus* workers between 16 August 1995 and 25 August 1995 at Cornell University's Liddell field laboratory in Ithaca, New York, U.S.A. Workers ($N=149$) were identified via thoracic marks made in early July or, when no mark was present, via wing wear and eye colour. All wasps were removed from single-queen colonies ($N=9$) located on the eaves of a shed, a barn and two wooden awnings, placed in plastic storage containers, cooled briefly (no more than 10 min, temperature=5°C) to facilitate handling, and organized into observation arenas in groups of two (dyad) or three (triad). A dyad ($N=22$) was composed of two worker wasps of similar size, either two nestmates or two non-nestmates. A triad ($N=35$) was composed of three worker wasps of similar size, two nestmates and one non-nestmate.

The wasps were placed in a clear plastic rectangular observation arena ($9 \times 6.5 \times 6.5$ cm) with two, full perimeter external markings dividing the container into three equal compartments. The arena size was selected to facilitate contact between wasps while providing room for the animals to move freely. Observers who were unaware of the animals' nest affiliations then recorded the spatial location (i.e. compartment) of each wasp every 2 min and all interactions for 60 min. To control for observer effects, each observer ($N=2$) scored a similar number of dyads (nestmate and non-nestmate) and triads. The following interactions were considered aggressive: darts (rapid movement towards a conspecific), lunges (a dart with contact), bites (mandible-to-body contact), mounts (one animal on top of another, forcing subordinate posture of the mounted animal), grapples (wrestling), stings (sting-to-body contact), and falling fights (escalated fight until both individuals fall). Antennations (antenna-to-antenna or antenna-to-body contact) were considered tolerant interactions (Pfennig et al. 1983; Reeve 1991). After each trial, all wasps were released and the containers cleaned with soap and warm water for future trials.

No worker was observed more than once. No two colonies were used in pairwise comparisons more than three times: once for dyad observations and twice for triad observations (each colony providing a nestmate group and a single non-nestmate for separate triads). Most individuals had a previous thoracic Testors enamel paint mark, and in the cases where there was not a previous mark, a distinctive thoracic mark was made just prior to observations. All observations took place indoors between 0900 and 1700 hours with an ambient temperature of $26.6° \pm 3.3°$C. We observed wasps for a total of 47 h and recorded 507 total interactions, 131 of which were aggressive.

Methods 1996

We used the same procedures as in 1995 with the following exceptions. Observations were made between 30 July 1996 and 16 August 1996. Experimental wasps were from 42 single-queen colonies collected at eight field sites in Ithaca, New York. An average of three colonies were collected before 0900 hours on the morning of each observation day. Colonies were kept at room temperature (23°C) in plastic storage containers. Wasps were identified as workers using eye colour and wing wear; the queen was previously marked. Prior to observations, all test wasps ($N=480$) were given a distinctive thoracic mark with a Speedball paint pen and placed in a clear observation arena ($9 \times 6.5 \times 4.5$ cm) subdivided with an external marking into two equal compartments. In 130 of the 180 trials, a nest fragment was placed in one of the compartments. The nest fragment was either familiar, that is, cut from a test wasp's nest, or unfamiliar. All nest fragments were 15–20 cells in size and contained eggs and larvae. No nest fragment was used more than once. All observations took place between 1100 and 1700 hours in a warm ($31° \pm 2.2°$C), brightly lit room. Wasps in dyads ($N=60$) and triads ($N=120$) were observed for 46 min. Six dyad contexts and 10 triad contexts were observed (Table 1). Observers ($N=3$) equally divided observations of all dyad and triad treatment combinations. Dyad and triad observations were temporally overlapped

Table 1. Combinations of individuals in dyads and triads for the 1996 study

	No nest fragment	Familiar nest fragment	Unfamiliar nest fragment
Dyads			
Nestmates	D1; $N=10$	D2; $N=10$	D3; $N=10$
Non-nestmates	D4; $N=10$	D5;* $N=10$	D6; $N=10$
Triads			
Nestmates	T1; $N=10$	T2; $N=15$	T3; $N=10$
Non-nestmates (all)	T4; $N=10$	T5;* $N=15$	T6; $N=10$
Two nestmates/one non-nestmate	T7; $N=10$	T8;† $N=15$	T10; $N=10$
		T9;‡ $N=15$	

*Nest fragment familiar to only one animal.
†Nest fragment familiar to nestmate pair.
‡Nest fragment familiar to the non-nestmate.

to control for differences in day-to-day variation in environmental factors affecting the behaviour of the animals. We observed wasps for a total of 138 h and recorded 8933 total interactions, 2402 of which were aggressive.

General Statistical Methods

Descriptive statistics are nontransformed means ($\pm$ SE). Prior to statistical testing, the number of aggressive or tolerant acts were transformed using the equation $\ln(1+X_n)$. Proportion data were transformed using the equation $\arcsin\sqrt{X_n}$, where X_n=the proportion of aggressive (or tolerant) behaviours between subjects divided by the total number of behaviours observed. We compared aggression both within and between dyad and triad systems using nonparametric Mann–Whitney tests. In triads containing a pair of nestmates and a single non-nestmate, we averaged the number of non-nestmate interactions across the two possible non-nestmate pairs prior to transformation of the mean. All tests were performed using Minitab 8.21 statistical software for the Macintosh.

Nest Fragment Association

An association was defined as an instance when an individual was in the same compartment as the nest fragment at the time of the scan. We performed 23 scans per 46-min trial and collected data on each animal in the observational arena. As such, each dyad supplied two data points and each triad three.

Neighbour Analysis

Individuals were considered neighbours if the nests from which they were taken were located on the same building or wooden awning (dyads, $N=6$; triads, $N=9$). The structures are situated in different regions of the field site such that individual colonies nesting on the same structure were, in all cases, much closer to each other (approximately 1.0–10 m) than to any colony on other structures (>45 m). Wasps were occasionally observed to interact with neighbour non-nestmates but not non-neighbour non-nestmates (personal observation). However, neighbour interactions were only observed on the structure where both nests were located. Any non-neighbour interactions probably occurred away from the colony (e.g. at common foraging grounds).

RESULTS

Nestmate Discrimination

In dyads without nest fragments, non-nestmate pairs were not more aggressive than nestmate pairs (Mann–Whitney test: 1995: $W=136.0$, $N_1=N_2=11$, NS; 1996: $W=112.5$, $N_1=N_2=10$, NS; Fig. 2). In contrast, in triads containing a nestmate pair, a non-nestmate and no nest fragment, non-nestmate interactions were significantly more aggressive than nestmate interactions (Mann–Whitney test: 1995: $W=1547.5$, $N_1=N_2=35$, $P<0.001$; 1996: $W=78.0$, $N_1=N_2=15$, $P<0.05$; Fig. 2). These results indicate that nestmate discrimination in *P. dominulus* is dependent on social context, specifically the number of nestmates present.

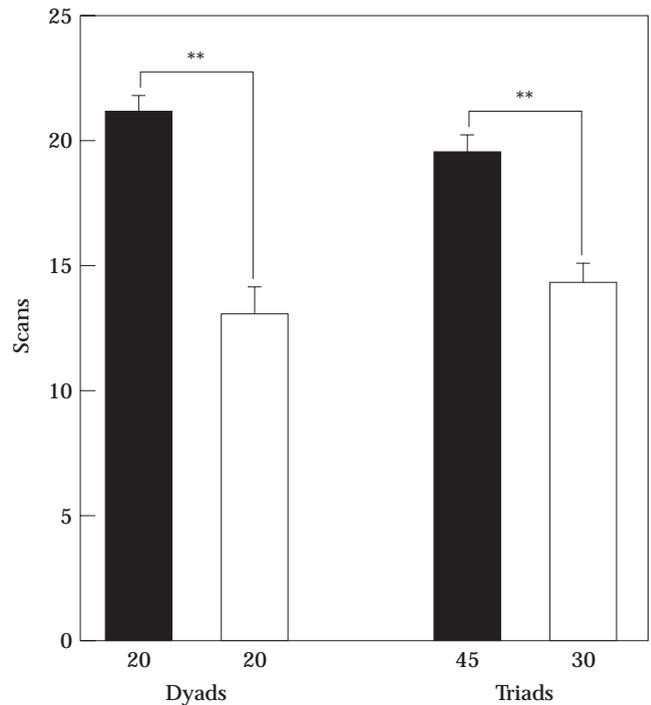### Mean Number of Aggressive and Tolerant Interactions

Significantly more darts and lunges, mounts, falling fights, stings and bites occurred between non-nestmates than between nestmates both in dyads with familiar nest fragments and triads with and without familiar nest fragments (Table 2). Grapples were more likely between non-nestmates than nestmates, but not significantly so. Antennations were no more likely between nestmates than non-nestmates. All levels of aggressive interactions were more common between non-nestmates than between nestmates.

Nest Fragment Association

Individuals were significantly more likely to associate with familiar nest material than with unfamiliar nest
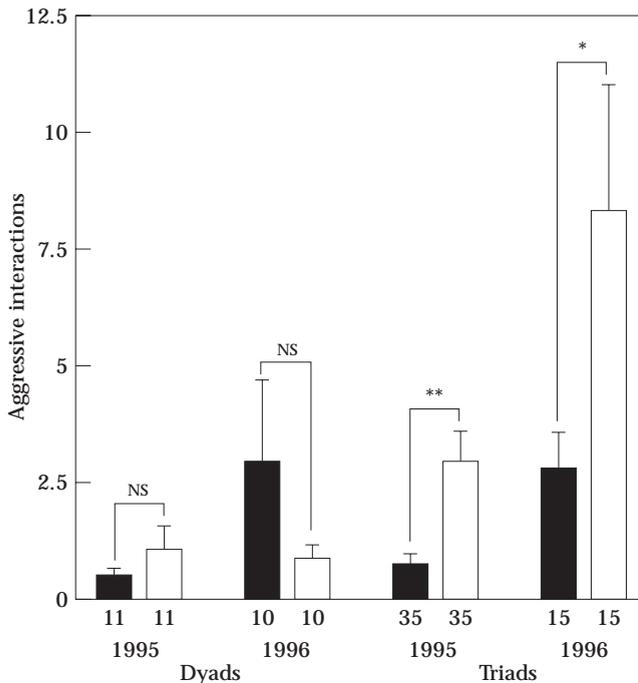
Figure 2. Mean (+SE) number of aggressive interactions between nestmates (■) and between non-nestmates (□) in dyads and triads without nest fragments. In triads, the number of interactions between non-nestmates was averaged prior to analysis. *N* values are listed under the appropriate column. Columns represent nontransformed means. NS: not significant, *$P<0.05$, **$P<0.001$.

Table 2. Mean (±SE) number of the different interactions between nestmate and non-nestmate pairs in dyads and triads displaying nestmate discrimination

Interaction	Nestmates ($N=50$)	Non-nestmates ($N=50$)	$P*$ value
Antennation	15.96 (2.09)	12.79 (1.97)	>0.10
Dart/lunge	3.54 (1.12)	6.08 (0.95)	<0.01
Mount	0.32 (0.17)	0.73 (0.12)	<0.01
Grapple	0.08 (0.05)	0.30 (0.12)	<0.10
Falling fight	0.00 (0.00)	0.46 (0.14)	<0.01
Bite	0.06 (0.03)	2.46 (0.49)	<0.01
Sting	0.00 (0.00)	0.52 (0.27)	<0.01

*Mann–Whitney tests.

material in both nestmate dyads and nestmate triads (Mann–Whitney test: dyads: $W=563.0$, $N_1=N_2=20$, $P<0.0001$; triads: $W=2163.0$, $N_1=45$, $N_2=30$, $P<0.0001$; Fig. 3).

Effects of Familiar Nest Fragments

Initiation of aggression

In nestmate/non-nestmate triads (Table 1, contexts T8 and T9), the individual(s) familiar with the nest fragment initiated significantly more aggressive interactions than those unfamiliar with the nest fragment (Mann–Whitney test: non-nestmate familiar: $W=303.0$, $N_1=N_2=15$,

Figure 3. Mean (+SE) number of scans during which an individual was observed in the compartment containing a familiar (■) or an unfamiliar (□) nest fragment. All data are from 1996. *N* values are listed under the appropriate column. Columns represent nontransformed means. **$P<0.0001$.

$P<0.01$; nestmate pair familiar: $W=161.0$, $N_1=N_2=15$, $P<0.01$; Fig. 4). *Polistes dominulus* defended a familiar nest fragment regardless of whether a nestmate was present.

Aggression in non-nestmate dyads

Aggressive acts were not more likely to occur between non-nestmates than between nestmates in dyads without nest fragments (Fig. 2), whereas aggressive acts tended to be more common between non-nestmates than between nestmates in dyads with familiar nest fragments (Mann–Whitney test: $W=128.0$, $N_1=N_2=10$, $P<0.10$; Fig. 5). The proportion of total interactions between non-nestmates that were aggressive was significantly higher in dyads with familiar nest fragments than in dyads without nest fragments (Mann–Whitney test: $W=59.0$, $N_1=N_2=10$, $P<0.001$; D5 versus D4 in Fig. 6). These results indicate that nestmate discrimination is displayed in dyads with familiar nest fragments.

Proportion of Aggressive Interactions Between Non-nestmates

Contexts D4, D5, T5, T7 and T8

We compared the proportion of total interactions that were aggressive between non-nestmates over five separate contexts (D4, D5, T5, T7 and T8; Fig. 6). We evaluated contexts with respect to the number of 'nest-indicators' (i.e. presence of nestmates and/or a familiar nest fragment) and 'threats' (i.e. the number of non-nestmates in
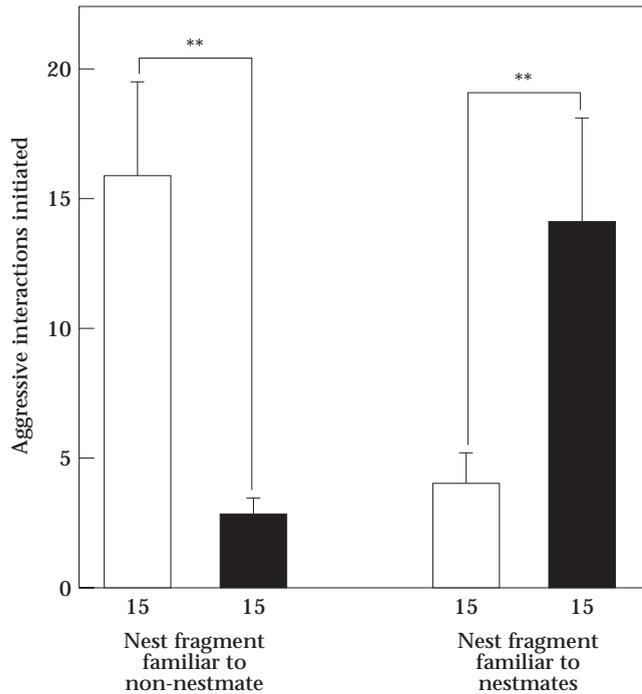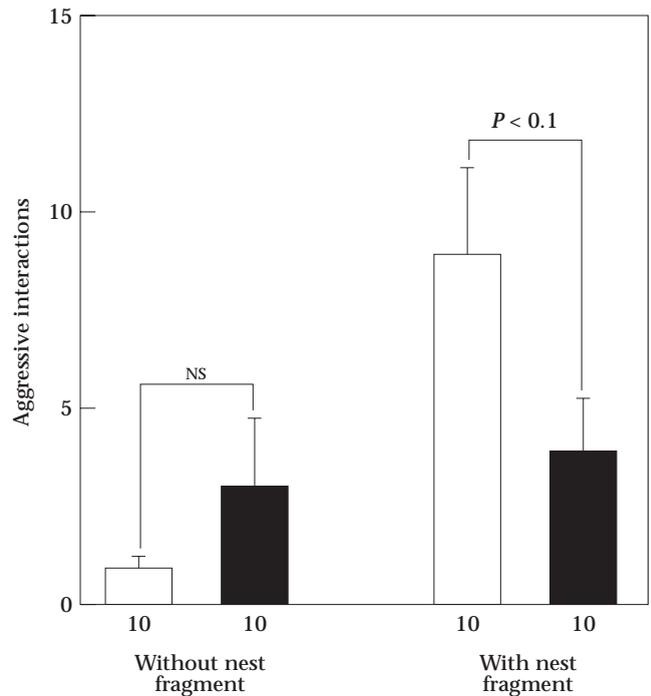
Figure 4. Mean (+SE) number of aggressive interactions initiated by the average member of a nestmate pair (■) and by the single non-nestmate (□) in triads with nest fragments familiar to either the nestmate pair or the non-nestmate. All data are from 1996. *N* values are listed under the appropriate column. Columns represent nontransformed means. **$P<0.01$.

Figure 5. Mean (+SE) number of aggressive interactions between pairs of nestmates (■) and non-nestmates (□) in dyads containing either no nest fragment or a nest fragment familiar to one of the wasps. All data are from 1996. *N* values are listed under the appropriate column. Columns represent nontransformed means.
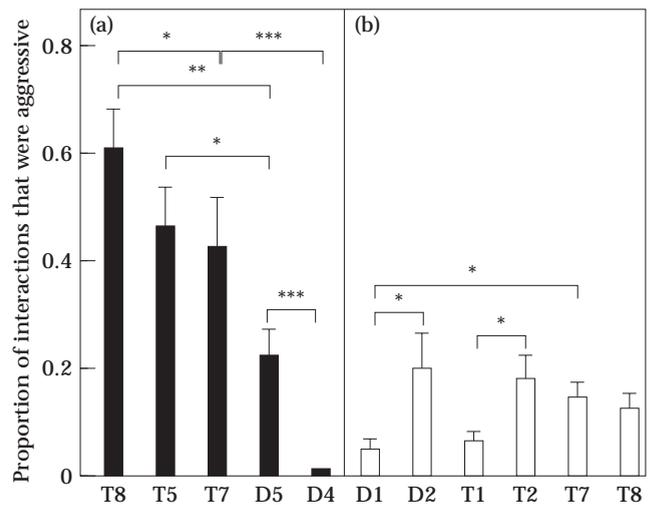
the system from the perspective of the individual(s) that had nest indicator(s) present). Aggression varied significantly between non-nestmates as a function of the number of nest indicators (Mann–Whitney test: T8 versus T7: $W=234.0$, $N_1=15$, $N_2=10$, $P<0.05$; T8 versus D5: $W=72.0$, $N_1=15$, $N_2=10$, $P<0.01$; Fig. 6), threats (T5 versus D5: $W=89.0$, $N_1=15$, $N_2=10$, $P<0.05$; Fig. 6) and a combination of the two (T7 versus D4: $W=61.0$, $N_1=15$, $N_2=10$, $P<0.001$; D5 versus D4: $W=59.0$, $N_1=N_2=10$, $P<0.001$; Fig. 6). Aggression between non-nestmates was highly sensitive to context.

Contexts D1, D2, T1, T2, T7 and T8

We compared the proportion of total interactions that were aggressive between nestmates over six separate contexts (D1, D2, T1, T2, T7 and T8; Fig. 6). Within dyads and triads, aggression was significantly higher between nestmates as the number of nest indicators increased (Mann–Whitney test: D1 versus D2: $W=74.5$, $N_1=N_2=10$, $P<0.05$; T1 versus T2: $W=89.0$, $N_1=10$, $N_2=15$, $P<0.05$; Fig. 6). In systems with one nest indicator, aggression increased significantly between nestmates when a threat was present (Mann–Whitney test: D1 versus T7: $W=71.0$, $N_1=N_2=10$, $P<0.05$; Fig. 6). No significant difference was observed in the proportion of aggressive interactions between nestmates comparing individuals in the remaining contexts. The presence of familiar nest fragments in all-nestmate dyads and all-nestmate triads increased aggression between nestmates.

Figure 6. Proportion of aggressive interactions between (a) non-nestmates and (b) nestmates in different contexts. Nest-indicators (NI) are nestmates and/or nest fragments; a threat (T) is a non-nestmate when a nest indicator is in the system. The number of NI and T for each context was; (a) T8: 2 NI, 1 T; T5: 1 NI, 2 T; T7: 1 NI, 1 T; D5: 1 NI, 1 T; D4: 0 NI, 0 T and (b) D1: 1 NI, 0 T; D2: 2 NI, 0 T; T1: 2 NI, 0 T; T2: 3 NI, 0 T; T7: 1 NI, 1 T; T8: 2 NI, 1 T. All values are from 1996. *N* values are as listed. Bars represent nontransformed means. *$P<0.05$, **$P<0.01$, ***$P<0.001$.

Neighbour Analysis

In triads, but not in dyads, significantly more aggressive behaviours were directed at neighbour
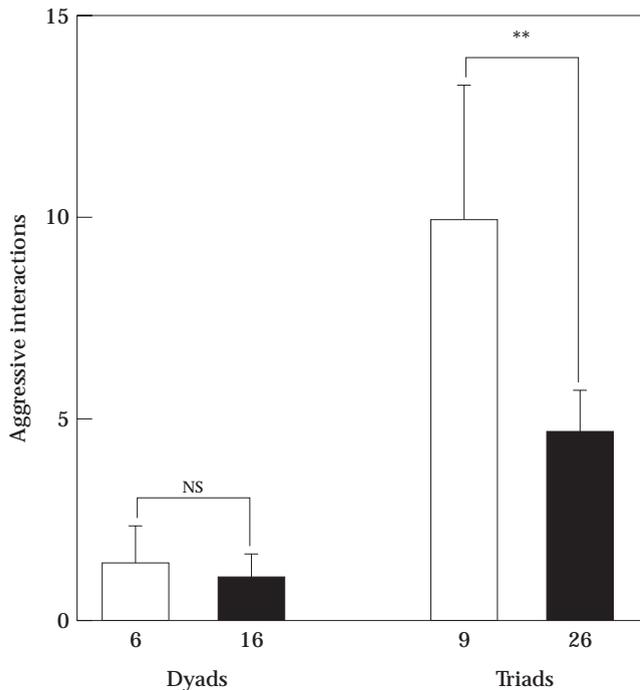
Figure 7. Mean (+SE) number of aggressive interactions between neighbour non-nestmates (☐) and between non-neighbour non-nestmates (■) in both dyads and triads. Aggression was significantly biased towards neighbours in triads, whereas no neighbour effect was observed in dyads. All data are from 1995. *N* values are listed under the appropriate column. The columns represent nontransformed means. **P<0.01.

non-nestmates than at non-neighbour non-nestmates (Mann–Whitney test: triads: $W=231.0$, $N_1=9$, $N_2=26$, $P<0.01$; dyads: $W=31.0$, $N_1=6$, $N_2=16$, NS; Fig. 7). These results suggest that *P. dominulus* discriminated against neighbours but only in some contexts.

DISCUSSION

Contrary to Pratte (1982), our results indicate that *P. dominulus* females have the ability to discriminate between nestmates and non-nestmates and that the behaviour is affected by context. Specifically, in the absence of nest fragments, wasps in triads displayed greater aggression towards non-nestmates than did wasps in dyads (Fig. 2). We tested two competing hypotheses to explain why the presence of a nestmate enhances aggression towards non-nestmates: the nest indicator and cost minimizer hypotheses.

Nest indicator Hypothesis

The nest indicator hypothesis suggests that the presence of a nestmate indicates that the nest is nearby, and there is therefore a fitness payoff for aggressive defence of the wasp's future reproductive relatives. Individuals in the presence of nestmates may be differentially aggressive towards non-nestmates as the latter may represent brood-robbing or usurpation threats (Kasuya et al. 1980; Gamboa et al. 1992). In contrast, individuals in dyads

may perceive themselves to be in a context where no such threat exists and therefore little aggression is directed towards non-nestmates.

Cost Minimizer Hypotheses

The cost minimizer hypothesis predicts that the presence of a nestmate triggers increased aggression towards non-nestmates because the cost of nest defence can be shared with the other nestmate. Individuals in the presence of nestmates may be differentially aggressive towards non-nestmates because the fitness payoff for shared defence outweigh the averaged cost of aggression between non-nestmates. Individuals in non-nestmate dyads may be unwilling to incur the full cost of aggression and therefore little aggression is observed. Because a wasp is more likely to encounter a nestmate on or near the colony than it is away from the colony, both the nest indicator and the cost minimizer hypotheses explain previous evidence that differential aggression towards non-nestmates increases with increasing proximity to the nest (Gamboa et al. 1991; Venkataraman & Gadagkar 1992).

Both hypotheses make specific, testable predictions. The nest indicator hypothesis critically predicts that a wasp will display enhanced aggression towards non-nestmates when cues suggest that the nest is nearby. Accordingly, a wasp should: (1) recognize its nest, (2) defend the nest and (3) display nestmate discrimination in dyads with familiar nest fragments and not in dyads without familiar nest fragments. The cost minimizer hypothesis predicts that, regardless of the presence or absence of familiar nest material, enhanced aggression towards non-nestmates should only be observed in systems with a nestmate pair. The hypotheses are most clearly in opposition with regards to observing nestmate discrimination in dyads. The nest indicator hypothesis predicts that nestmate discrimination will be observed in dyads containing cues indicating close proximity to the nest, whereas the cost minimizer hypothesis predicts that nestmate discrimination will not be observed in dyads consisting of non-nestmates.

To test prediction 1 of the nest indicator hypothesis, we divided the observation chamber into two compartments and placed either a familiar or an unfamiliar nest fragment into one of the compartments. Our results indicate that workers will preferentially associate with their own nest fragment (Fig. 3). Note that all nest fragments contained brood, so we could not distinguish between brood and nest paper recognition.

To test predictions 2 and 3 of the nest indicator hypothesis and the cost minimizer hypothesis, two triad contexts (T8 and T9) were devised. In half of the triads, the nestmate pair was familiar with the nest fragment, and in the other half, the non-nestmate was familiar with the fragment. The nest indicator hypothesis predicts that the majority of aggressive interactions will be initiated by the individual(s) that are familiar with the nest fragment, whereas the cost minimizer hypothesis predicts that the majority of aggressive interactions should be initiated by

the nestmate pair. Our results showed that the individual(s) that was familiar with the nest fragment initiated significantly more aggressive interactions (Fig. 4), thus supporting the nest indicator hypothesis.

Finally, to test critically prediction 3 of the nest indicator hypothesis and the cost minimizer hypothesis, we examined aggression between non-nestmates in dyads containing either no nest fragment or a familiar nest fragment. The nest indicator hypothesis predicts that presence of a familiar nest fragment should increase aggression between the non-nestmates, whereas the cost minimizer hypothesis predicts no such increase. Nestmate discrimination was not displayed in dyads without nest fragments (Figs 2, 5, 7). Individuals in dyads with familiar nest fragments, however, displayed a strong trend towards nestmate discrimination (Fig. 5). This result, coupled with a significantly higher proportion of aggressive interactions between non-nestmates in dyads with versus without familiar nest fragments (Fig. 6), supports the nest indicator hypothesis rather than the cost minimizer hypothesis.

The cost minimizer hypothesis could make similar predictions to the nest indicator hypothesis if one assumes that the presence of the nest indicates that nestmates are nearby and will engage in, and thus share the costs of, aggressive non-nestmate interactions. However, in this scenario, nestmates in the absence of familiar nest material should be about as aggressive to a non-nestmate as is a single non-nestmate, in the presence of its nest, to a pair of foreign nestmates. Our data show that the single non-nestmate in the presence of its nest initiates a significantly larger number of aggressive interactions than does the nestmate pair (Fig. 4).

A third hypothesis, the recognition template enhancement hypothesis, can also be excluded. This hypothesis suggests that the addition of a nestmate or familiar nest fragment will enhance the ability to detect non-nestmates because a nestmate or familiar nest fragment acts as a referent to which the non-nestmate can be compared. However, three lines of reasoning argue against the recognition template enhancement hypothesis: (1) the recognition template in *Polistes* develops within hours after a wasp emerges as an adult (Pfennig et al. 1983); (2) contrary to our results (Fig. 4), no difference between a nestmate pair and a single non-nestmate in aggressive acts initiated should be observed when a nestmate pair interacts with a single non-nestmate in the presence of the non-nestmate's nest fragment; and (3) instead of increased aggression (Fig. 6), aggression between nestmates should decrease with an increase in the number of nest indicators (i.e. the animals should become increasingly better at discriminating between nestmates and non-nestmates).

Our results strongly suggest that *P. dominulus* can recognize nestmates and that whether or not they exhibit behavioural discrimination between nestmates and non-nestmates depends on the presence of cues indicating the nest is nearby. Thus, the shift in the action component from recognition without discrimination to recognition with discrimination appears to be a function of cues related to the nest. As such, the context where nestmate discrimination is most likely to be observed is when the animal is on or near its colony. We tested two competing hypotheses to explain the behaviour of *P. dominulus* when the animal is in the discrimination context: the fixed error and optimal acceptance threshold model hypotheses.

Fixed Error and Optimal Acceptance Threshold Hypotheses

The fixed error and optimal acceptance threshold hypotheses predict that a wasp will recognize non-nestmates and aggress against them either alone or cooperatively with other nestmates. However, since no recognition system is perfect (Reeve 1989; Sherman et al. 1997), the discriminating wasp is likely to make errors, that is, occasionally aggress nestmates or tolerate non-nestmates. The fixed error hypothesis predicts that discrimination errors will occur at a constant frequency, and thus will not vary across contexts. Alternatively, the optimal acceptance threshold hypothesis predicts that the frequency of discrimination errors is dependent on the fitness costs of accepting non-nestmates and rejecting nestmates, and thus will vary with fitness costs associated with different contexts (Fig. 1).

The fixed error and the optimal acceptance threshold hypotheses generate competing predictions. The optimal acceptance threshold hypothesis predicts that the probability of rejection errors increases with the cost of acceptance errors (Reeve 1989). Consequently, in contexts where the wasp becomes more discriminating, aggression between nestmates (i.e. rejection errors) should increase. The fixed error hypothesis makes no such prediction, thus aggression between nestmates is not expected to change with the context.

A comparison of aggression between nestmates in different discriminating contexts represents a critical test of both hypotheses. Aggression between nestmates increased significantly with the number of cues indicating proximity to the nest and increased when a threat was present (Fig. 6). As this first context indicates an increased probability that the nest is nearby and the second context indicates a potential cost to the colony, both contexts can be interpreted as indicating increased costs of acceptance errors. Our results support the optimal acceptance threshold hypothesis.

Aggression did not vary significantly between every context, however, 0.2–0.25 appears to be an upper limit on the proportion of aggression between nestmates (Fig. 6). The results suggest that the presence of more than one nest indicator has no additive effect with respect to aggression between nestmates and that the presence of either nest indicator (nestmate or nest fragment) is sufficient to facilitate nestmate discrimination.

The fixed error hypothesis could be resurrected by suggesting that 'activation' aggression between nestmates is necessary to initiate cooperative nest defence, and that the level of activation varies according to context. Thus, the change in aggression levels between nestmates is the sum of the baseline (fixed) error and activation aggression. If this were true, enhanced aggression between

nestmates should only be observed when activation is necessary (i.e. when a threat is present), not in all-nestmate tests (Fig. 6). In addition, if activation aggression is necessary to initiate cooperation, low-level aggressive actions, such as darts and lunges, would be expected to be more frequent between nestmates than between non-nestmates (the conspiratorial whisper concept). Our data do not support that prediction. All aggressive interactions, including low-level aggressive activity, were more frequent between non-nestmates than between nestmates (Table 2). To suggest that these darts still represent activation aggression, one must assume either that the animals are making a vast number of activation mistakes by darting at non-nestmates or that the meaning of a dart between nestmates is different than a dart between non-nestmates. Although we have not directly tested the possibility of different dart meanings, we did not observe different immediate responses of dart recipients to darts from nestmates or non-nestmates.

An alternative to the optimal acceptance threshold hypothesis for increased aggression between nestmates is that increased aggression between nestmates resulted from re-establishing a dominance hierarchy. This hypothesis is consistent with the results that the proportions of aggression between the nestmates increases as cues suggest more strongly that the nest is nearby (Fig. 6). However, two lines of reasoning argue against a dominance hierarchy hypothesis. First, dominance between workers is a function of possible queen replacement and older wasps, not larger wasps, are more likely to replace queens (Hughes & Strassmann 1988). In our experiment, the test animals were of comparable size and the colonies collected often had more than 90 wasps. As older dominant wasps tend to be smaller than their nestmates (Hughes & Strassmann 1988), the probability is low that we selected a dominant wasp for observations. The second argument is that the dominance hierarchy hypothesis cannot explain why aggression remained high between nestmates when a non-nestmate was present. The maintenance of aggression between nestmates when threats are present is, however, predicted by the optimal acceptance threshold model (Reeve 1989). The results of our comparisons of aggression between nestmates are most consistent with the optimal threshold hypothesis.

Our design also enabled us to compare the proportion of aggression between non-nestmates in different contexts. Aggression between non-nestmates increased significantly with the number of threats (Fig. 6). This result is explicitly predicted by Reeve's model (Fig. 1): thresholds should become more restrictive when the frequency of contact with non-nestmates increases. Similarly, the proportion of aggression between non-nestmates increased with the number of nest indicators, that is, the threshold became more restrictive as cues suggested more strongly that the nest was nearby. Interestingly, the proportion of aggression was very low in non-nestmate dyads without a nest indicator (Fig. 6), lower, but not significantly so, than the proportion of aggression between nestmates in dyads with a nest indicator (the other nestmate; Fig. 6).

Combined, the between-nestmate and between-non-nestmate proportional results strongly support the optimal threshold model hypothesis rather than either the fixed error or dominance hierarchy hypotheses. These results may also lend considerable insight as to the distribution of recognition cues. The frequency distributions of nestmate recognition and non-nestmate cue-recognition should occupy different ranges on the dissimilarity index (Fig. 1). The acceptance threshold is the balance point of the costs of acceptance and rejection errors. Universal rejection of non-nestmates may coincide with a maximum level of aggression between nestmates, that is, there is no additional payoff for the aggression regardless of the context.

We have found critical support for the optimal acceptance threshold model. Although previous research has obtained results consistent with acceptance threshold shifts (see Gamboa et al. 1991; Fishwild & Gamboa 1992; Venkataraman & Gadagkar 1992), we believe this to be the first critical test of the model. Our results suggest that once in a discriminating context, nestmate discrimination in *P. dominulus* is best described by an acceptance threshold. The proportion of aggressive interactions between non-nestmates and between nestmates was very sensitive to context (Fig. 6). Thus the shift in the acceptance threshold appears to move at fine gradations, suggesting that the animals are responding adaptively to changes in their environment.

Neighbour Discrimination

Polistes dominulus can recognize neighbours, but whether they discriminate against them also depends on context: they act more aggressively towards neighbours than non-neighbours in triads but not in dyads (Fig. 7). Because neighbouring colonies share their immediate environment and may be closely related (West-Eberhard 1969; Strassmann 1979, 1983), it is unlikely that the recognition cues between neighbouring non-nestmates are more dissimilar than between non-neighbouring non-nestmates. Something more than a simple shift in an acceptance threshold may be occurring. This may instead be a context where it is beneficial to be especially aggressive towards non-nestmate kin (or nonkin). Discriminating especially against neighbours (even closely related neighbours) would be beneficial if the probability of a close neighbour stealing brood is sufficiently high, or if neighbouring colonies are competing in some other manner (Kasuya et al. 1980; Gamboa et al. 1992). Our findings suggest that the animals learn the phenotypic cues of neighbours (which they are more likely to encounter) and modify their interactions based on those cues.

Our results in *P. dominulus* differ from those of Pfennig (1990), which showed that *P. exclamans* display greater tolerance of neighbours than non-neighbours. The neighbours in Pfennig's study may have been more closely related than non-neighbours and, if there is a genetic basis to the recognition cue, may have been frequently mistaken as nestmates (i.e. the neighbour's cues were not learned). Our laboratory is currently examining neighbour relatedness in *P. dominulus*.

Conclusion

Our results indicate that *P. dominulus* workers can recognize and discriminate nestmates from non-nestmates, familiar from unfamiliar nest fragments, and neighbours from non-neighbours. Our findings suggest that nestmate and neighbour discrimination are context-dependent: discrimination occurs when either the presence of a nestmate or a nest fragment indicate the proximity of the colony. In addition, context-dependent variation in aggression levels is best described by a shift in an acceptance threshold. This study represents the first critical examination of Reeve's (1989) optimal acceptance threshold model.

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