



Division of labour in colony defence against vertebrate predators by the social wasp *Polistes fuscatus*

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In this study I examined how the paper wasp, *Polistes fuscatus*, defends a colony when faced with a vertebrate attack. I looked for a division of labour in defensive behaviour within a colony and examined whether this behaviour changes over the colony cycle. The colonies were presented with a model of an adult red-winged blackbird, *Agelaius phoeniceus*, and a speaker that vibrated the comb. There was a pronounced division of labour in the defence against vertebrate predators within a colony. The queen was consistently the most aggressive individual in the colony. The subordinate foundresses and workers both became more aggressive towards a vertebrate predator as they aged. Gynes and males did not participate in colony defence. The level of aggression in colony members of *P. fuscatus* appears to be related to the reproductive investment of the colony.

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Many eusocial species tend to have specialized castes of workers that defend the colony (Michener 1974). Termites (Bartz 1979; Gerber et al. 1988), social aphids (Aoki 1987; Stern & Foster 1996), social thrips (Crespi 1992) and some ants (Hölldobler & Wilson 1990) produce soldiers that defend the colony from insect and vertebrate attacks. Some species of ants show a distinct polymorphism among workers with larger individuals specialized as guards (Hölldobler & Wilson 1990). In naked mole-rat, *Heterocephalus glaber*, colonies the larger members of the colony tend to defend the colony (Lacey & Sherman 1991). *Apis mellifera* (Robinson & Page 1988), *Bombus bombus* (Michener 1974) and some Vespids (Akre & Reed 1984) have guards that are more likely to attack intruders than are other members of the colony. In swarm-founding wasps such as *Polybia occidentalis*, older individuals tend to defend the colony more than the younger individuals (Jeanne et al. 1992).

In the eusocial genus *Polistes*, however, there is no evidence for specialized castes of guards (West-Eberhard 1969), although there are certain cases where workers specialize when foraging (O'Donnell 1998). Workers of primitively eusocial insects are morphologically and reproductively similar to the queen and as a result, the workers of primitively eusocial colonies are not as

restricted as those of highly eusocial colonies. The decision rule on whether or not to defend a colony might be different for an unspecialized worker of *Polistes* than for a specialized worker of a highly eusocial species.

Vertebrate predators can significantly affect the survivorship of *Polistes* colonies (Turillazzi 1984; Starr 1985). Mammals such as foxes (Yamane & Kawamichi 1975) and rodents (Reed & Vinson 1979) have been observed attacking and eating *Polistes* colonies. Birds such as the red-winged blackbird, *Agelaius phoeniceus*, the Baltimore oriole, *Icterus galbula*, the scarlet tanager, *Piranga olivacea*, and the northern cardinal, *Cardinalis cardinalis*, are among the many birds that have been reported to attack *Polistes* colonies in North America (Gibo 1978; Turillazzi 1984). A single attack from a vertebrate can completely destroy the nest and eliminate the reproductive investment of the individuals in the colony (Starr 1985). Strassmann (1981) reported that birds cause a large proportion of *P. exclamans* colony failures by knocking down a nest and killing some wasps in the process. In temperate climates this could potentially eliminate any possibility of successfully reproducing for that year, and in the case of *Polistes*, the individual's life.

Judd (1998) showed the composite behaviour of *P. fuscatus* colonies change over the colony cycle, with increasing aggression over time. This suggests the individuals might be changing their behaviour as well. I used a consistent and repeatable simulated vertebrate stimulus (Judd 1998) to look for a division of defensive labour in *P. fuscatus* within a specific time period as well as to

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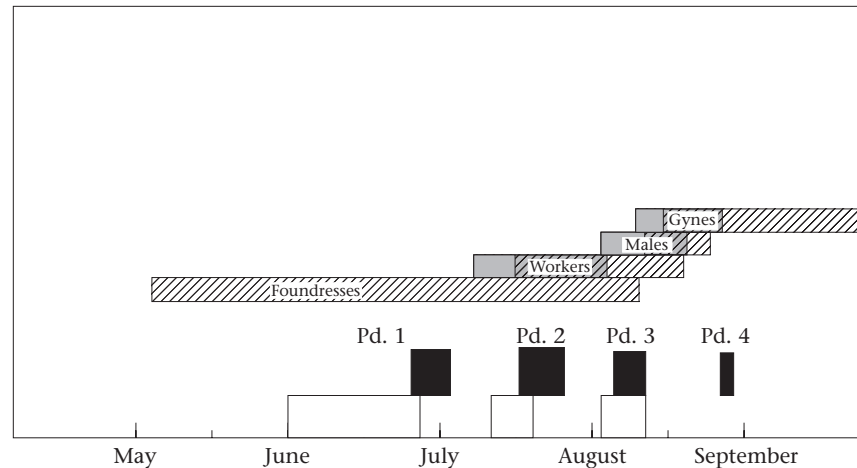


Figure 1. The colony cycle of *P. fuscatus*. The top four rows of bars show when each caste is found on the nest during the colony cycle (after Gamboa et al. 1991; Judd 1998). Shaded areas represent pupae and hatched areas indicate adults. Also shown are the experimental periods (1–4), during which behavioural observations (□) and simulated vertebrate attacks (■) were conducted.

examine the changes in individuals' defensive behaviour over the colony cycle.

METHODS

Study Sites

The project took place at two study sites (see Gamboa et al. 1992; Judd 1998). Study site 1 was located at Oakland University, Rochester, Michigan in a natural area on campus. Study site 2 was located in Metamora, Michigan on private property. The colonies of *P. fuscatus* were naturally founded in plywood nestboxes placed along the tree line in both sites. The colonies at site 2 were developmentally about a week behind those of the colonies at site 1.

General Procedures

I marked wasps for individual identification with Testors[®] model paint. Foundresses were marked at sunrise on 25 May (site 1) and 8 June (site 2) 1995. Workers were marked for individual identification on 7–8 July (site 1) and 13–14 July (site 2); these will be referred to as older workers. Unmarked workers that emerged later on the same colonies were painted 30–31 July (site 1) and 2–3 August (site 2); these will be referred to as younger workers.

I observed each colony during four periods, corresponding to the following phases of the colony cycle (Fig. 1; Judd 1998).

- Period 1: preworker emergence (only foundresses were present).
- Period 2: older worker emergence (approximately 5–7 days after the first workers emerged).
- Period 3: younger worker emergence (approximately 2–3 weeks after the first workers emerged).
- Period 4: reproductive phase (predominantly reproductives were on the nest).

Estimation of Dominance

Polistes wasps are known to form linear dominance hierarchies (Pardi 1948; Pratte 1997). These hierarchies form among foundresses and among workers, but workers are always subordinate to foundresses (Reeve 1991). In Period 1, I calculated a dominance index (*DI*) as described in Gamboa & Stump (1996) to determine the dominance hierarchy among cofoundresses. The *DI*, which incorporates both time on the nest and interactions, ranges from 0 to 1. The higher the *DI*, the more dominant the individual.

For Periods 2 and 3, because of the large number of individuals on the nest at this time in the colony cycle, I only observed the amount of time that individuals spent on the nest, not the number of interactions that occurred. Thus, the *DI* is simply the proportion of observation time the individual was on the nest. The amount of time spent on the nest corresponds to the dominance level of a wasp (Pardi 1948). Furthermore, I did not calculate dominance for individuals (reproductives) in Period 4.

For Period 1, I observed each multiple-foundress colony for 4 h to determine the dominance rank of each cofoundress. For Period 2, I observed each colony for 2 h, and for Period 3, I observed each colony for 1 h (Fig. 1). I observed a total of 30 colonies. Of these, 17 colonies were multiple-foundress colonies (12 two-foundress, 3 three-foundress, 2 four-foundress, and 1 six-foundress colony). Over the course of the study, one colony failed and several foundresses disappeared (Periods 2–3). I made a total of 158 h observation on the colonies.

Presentation of the Simulated Vertebrate Predator

The simulated attack by a vertebrate predator consisted of both a visual and a vibrational stimulus because most wasps also are highly sensitive to nest vibrations (Jeanne 1982). The visual stimulus was a three-dimensional, life-sized model of a male red-winged blackbird (Judd 1998).

The vibrational stimulus was provided by a speaker temporarily mounted on the nestbox (Judd 1998). I used a cassette recorder to send a bass beat through the speaker at 160 beats/min.

Before the presentation of the visual and vibrational stimuli, I recorded the identity of all individuals present on the nest. I presented the model bird 15 cm from the nest together with the vibration stimulus. During the presentation, I moved the model towards and away from the nest at the same frequency as the beat in the speaker. The simulated attack lasted 20 s. In a natural situation this would represent a bird trying to peck and knock the nest down.

I recorded the response of each individual on the nest to the simulated attack on audio tape, which I later transcribed. I conducted simulated attacks on each colony only once in each of the four time periods to minimize the possibility that the wasps would habituate to the simulation. There was at least a 10-min interval between presentations at different nests, minimizing any possible effects of an alarm pheromone (Post et al. 1984; Matthews & Matthews 1988).

Estimation of Aggression

The simulated attack elicited five different responses from the wasps. I ranked the responses subjectively based on the level of aggression they represented (cf. Starr 1990) from the least aggressive (1) to the most aggressive (5) as follows.

- (1) Wasps abandoned the nest, flying away from the model.
- (2) Wasps remained immobile or oriented towards the bird model.
- (3) Wasps waved their front legs or displayed wing flipping (wing buzzing).
- (4) Wasps left the nest, approached and circled the model.
- (5) Wasps left the nest and stung the model.

I used these behaviours to assign each individual an aggression index (*AI*) based on its behavioural response to the simulated vertebrate attack.

Data Analysis

When comparing the aggression indices between castes or age groups, I used the median as a measure of the central tendency. This allowed me to compare castes with small numbers of individuals (e.g. queens) with those castes having large numbers of individuals (e.g. workers). I analysed the data in three ways to examine: differences among castes for each time period, differences over the colony cycle for each caste, and trends over the colony cycle for individual wasps.

I also examined whether queens or workers were the first to respond (come off the nest) aggressively during a simulated attack. I ranked the workers and queens according to the numerical order in which they left the nest. Individuals that came off the nest at the same time were

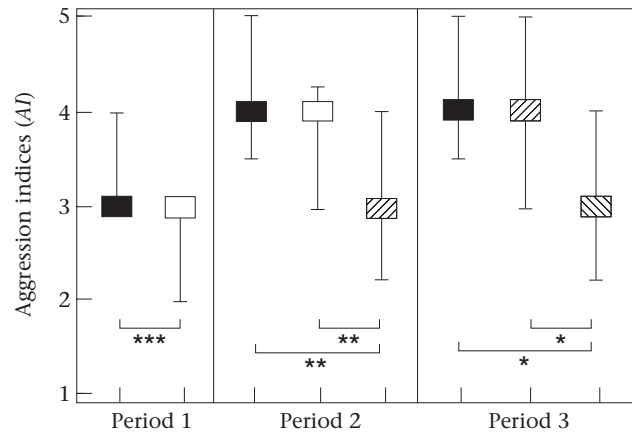


Figure 2. Comparisons of the median aggression indices (*AIs*: 1–5, 1=least, 5=most aggressive) and the quartile ranges for different castes of *P. fuscatus* during Periods 1–3. ■: Queens; □: subordinate foundresses; ▨: old workers; ▩: young workers. * $P < 0.05$, ** $P < 0.01$, *** $P < 0.006$.

given an average rank. Queenless colonies and colonies without aggressive individuals were eliminated from the calculations.

RESULTS

Division of Labour between Castes

In Period 1 queens had significantly greater *AIs* than the subordinate foundresses (Fig. 2) (Wilcoxon signed-ranks test: $T = 4.56$, $N = 16$, $P = 0.006$). In Period 2 the *AIs* of the queens and the subordinate foundresses did not differ but the queens had significantly greater *AIs* than the older workers (Friedman test and multiple comparison procedure: $W = 0.511$, $N = 9$, $P < 0.01$). Although subordinate foundresses had greater *AIs* than the workers in Period 2, the difference was not significant. In Period 3, there were insufficient numbers of subordinate foundresses to make a meaningful comparison between queens and subordinates. *AIs* for queens were similar to old workers, and both were significantly larger than *AIs* for young workers (Friedman test and the multiple comparison test procedure: $W = 0.346$, $N = 10$, $P = 0.05$; Fig. 2).

Queens did not come off the nest aggressively before workers in Period 2 (Wilcoxon signed-ranks test; Table 1), but they did in Period 3 ($T = 7$, $N = 13$, $P = 0.025$; Table 1).

Behaviourally, the workers seemed to fall into three distinct categories (and three distributions) that correlated with their dominance ranks. Thus the workers were divided into three categories based on dominance ranks: low-ranked individuals ($DI = 0–0.2$); middle-ranked individuals ($DI = 0.21–0.79$); and high-ranked individuals ($DI = 0.8–1.0$). Low-ranked individuals were the chief foragers. High-ranked individuals spent most of their time unloading food from returning foragers and feeding the larvae. The middle-ranking individuals participated in both of these tasks. I compared the three groups of workers using the Friedman test for Period 2 and Period 3 in colonies that contained high-, middle-, and low-ranking

Table 1. Comparison to determine whether *P. fuscatus* queens tend to respond to a simulated predator before workers

Observation period	N	Mean±SD queen rank	Mean±SD worker rank	<i>P</i> *
Period 2	16	3.29±2.2	3.40±1.0	NS
Period 3	13	2.80±2.2	3.95±1.3	0.025

Queens and workers were ranked according to the numerical order in which they left the nest (i.e. responded aggressively).

*Wilcoxon signed-ranks test.

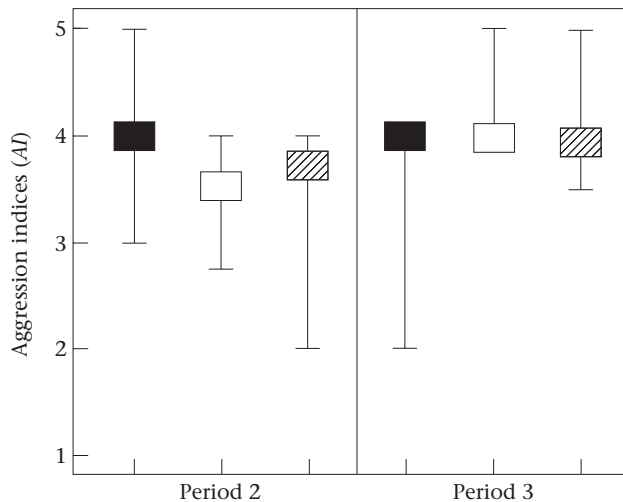


Figure 3. Comparisons of the median aggression indices (*AIs*: 1–5, 1=least, 5=most aggressive) of high- (■), middle- (□), and low-ranking (▨) workers for Periods 2 and 3. In both cases there were no significant differences between the aggression indices of the three groups of workers. Period 2: Friedman test: $W=0.16$, $N=10$, NS. Period 3: Friedman test: $W=0.255$, $N=11$, NS.

individuals. In both periods, there was no difference in *AI* among the dominance ranks (Fig. 3).

In addition I examined whether older workers tended to have higher dominance indices than younger workers. There was no significant differences between older worker and younger worker dominance indices (Mann–Whitney U test: $Z=0.996$, $N_1=97$, $N_2=23$, NS).

Caste-specific Changes in Aggression through the Colony Cycle

I compared caste-specific changes in aggression over time using the multirange permutation procedure (MRPP; Riech et al. 1990, 1991). The distribution of the queens' aggression indices changed significantly from Period 1 to Period 3 (MRPP: $M=-8.98$, $N_{P1}=30$, $N_{P2}=25$, $N_{P3}=19$, $P=0.001$; Fig. 4), with higher *AIs* over time. In fact, most queens stung the model in Period 3 (Fig. 3). Only three queens remained by Period 4 and all three stung the model during the simulated attack. The distribution of the *AIs* of subordinate foundresses also increased significantly from Period 1 to Period 2 (MRPP: $M=-16.25$,

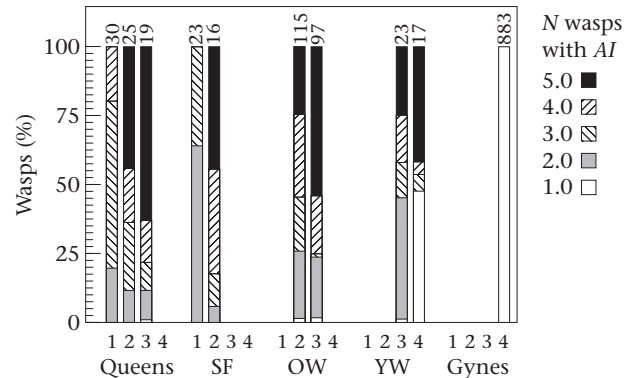


Figure 4. The distribution of the aggression indices of queens, subordinate foundresses (SF), older workers (OW), younger workers (YW) and gynes over the colony cycle (Periods 1–4). Multirange permutation procedure: queens ($P=0.001$), SF ($P<0.0001$), OW ($P<0.0001$) and YW (NS). The numbers above the bars indicate the number of individuals represented.

$N_{P1}=23$, $N_{P2}=16$, $P<0.0001$); most of these disappeared from the colony by Period 3. Older workers showed a significant increase in aggression from Period 2 to Period 3 (MRPP: $M=-8.37$, $N_{P2}=115$, $N_{P3}=97$, $P<0.0001$). Although the younger workers tended to be more aggressive in Period 4 than in Period 3, the difference was not significant (MRPP: $M=-1.02$, $N_{P3}=23$, $N_{P4}=17$, NS). Therefore all groups showed increasing aggression over time.

By contrast, gynes ($N=883$) and males ($N=312$) always abandoned the nest as soon as the simulated attack started and thus did not participate in colony defence (Fig. 4).

Individual Changes in Aggression through the Colony Cycle

I also tracked individual wasps to examine individual changes in aggression over time. The sample sizes for these comparisons were low because individuals disappeared over the season. Individual queens showed a significant increase in aggression from Period 1 to Period 2 (Wilcoxon signed-ranks test: $T=34$, $N=18$, $P=0.012$) but did not show a significant increase from Period 2 to Period 3 ($T=12$, $N=7$, $P=0.4$). Subordinate foundresses showed a significant increase in aggression from Period 1

to Period 2 ($T=4$, $N=11$, $P=0.0034$). Older workers also showed a significant increase from Period 2 to Period 3 ($Z=1.72$, $N=31$, $P=0.043$). These results are similar to those of the caste-level analysis.

DISCUSSION

Three main patterns emerged in my study of the defensive behaviour of individual *P. fuscatus* against vertebrate predators: (1) the primary reproductive, the queen, was either the most aggressive wasp or among the most aggressive wasps in response to a simulated vertebrate predator; (2) queens, subordinate foundresses and workers became more aggressive towards a vertebrate predator as they became older; (3) gynes and males did not participate in colony defence.

Colony defence in *P. fuscatus* differs from most other social insects in that the queen actively participates in colony defence. Insects such as termites, ants, bees and many wasps have specialized workers that defend the colony, and typically the queen does not participate in colony defence at all (Michener 1974). Not only did the *P. fuscatus* queens in this study have a higher *AI* than most of the subordinate foundresses and workers, the queen was among the first wasps to initiate an attack in Period 3. This is the first recorded case in wasps where the queen of the colony remains aggressive against vertebrates throughout the colony cycle. However, Fishwild & Gamboa (1992) found that *P. fuscatus* queens were also the most aggressive individuals towards unrelated conspecifics.

The change in behaviour over time shown by subordinate foundresses and workers of *P. fuscatus* presents an interesting problem. Because a nest destroyed by a vertebrate predator is completely lost, why would some workers hold back from defending the nest? It has been assumed in the past that workers have no other option but to stay and help at the nest (Wilson 1971). Although there are some subtle differences between *Polistes* queens and workers (Pardi 1948), both are believed to be capable of initiating a colony (Noonan 1979; but see O'Donnell 1998). Evidence exists for three possible alternative options for workers. Females produced in the early spring could form satellite nests (Owen 1962; Page et al. 1989). A second possibility is to join a sister colony. In some instances workers shift between two highly related colonies (personal observation). These cases are uncommon, as most colonies are very intolerant of non-nestmates (Gamboa et al. 1992). A third option for workers is to mate and go into diapause and become a foundress the following year. It has been observed that some workers disappear early in the colony cycle. A few of these missing workers have been observed the following spring as foundresses (G. J. Gamboa, personal communication) or observed overwintering with gynes in a hibernaculum (H. K. Reeve, personal communication). Yanega (1988) found that some workers of the primitively social bee *Halictus rubicundus* left the colony and went into early diapause, returning the following spring to initiate their own colonies. Although rare, alternatives for workers do exist.

There was a strong relationship between the aggressiveness and age of the individual in queens, subordinate foundresses and older workers. This was demonstrated by the caste-level analysis as well as the individual-level analysis. Temporal polyethism, the change in behaviour as an individual ages, has been seen in many species of social insects where older, more expendable individuals take on more life-threatening tasks (West-Eberhard 1969; Oster & Wilson 1978; Jeanne 1991; Bourke & Franks 1995). In ants (Dejean & Lachaud 1991; Bourke & Franks 1995), termites (Gerber et al. 1988; Noirot 1989), honeybees (Seeley 1985; Robinson et al. 1994) and swarm-founding wasps (Jeanne et al. 1992), older individuals do the majority of the foraging and defending. Although some of the data in this study fit this pattern, the role of the *P. fuscatus* queen does not; the *P. fuscatus* queen aggressively defends the nest but she is not expendable. In the aforementioned highly eusocial insect colonies there are larger numbers of individuals to defend the nest, so the risk of attacking may be less per individual. In *P. fuscatus* there are smaller numbers of defenders so the risk per individual is much greater given that wasps are killed by birds during attacks on the nest (Strassmann 1981). In large colonies the lack of queen participation in defence would have little consequence, whereas in small colonies such as *Polistes*, the queen's participation may make a difference.

Ultimately there are two forces that could drive the change in aggression in *Polistes* wasps. First, the aggression levels of individuals increase with the amount of personal investment in the nest. For example, the solitary digger wasp, *Sphex ichneumoneus*, will fight harder for her nest, as the amount of provisions she gathers increases (Dawkins & Brockmann 1980). Second, opportunities for colony founding decrease over time due to physical degradation (O'Donnell & Jeanne 1995) and limited nesting season (Noonan 1979). Like many insects, wasps are unable to repair muscles and other body parts (Kurkut & Gilbert 1985) and as a result, most workers have short lives (about 4 weeks; Reeve 1991). In addition, as chances of successfully initiating a new colony in the later stages of the colony cycle decrease due to seasonal time constraints (Noonan 1979), the nest becomes increasingly more valuable. In the *S. ichneumoneus* example, wasps experience physical degradation and have a limited amount of time to build a successful nest. Indeed, *P. fuscatus* colonies as a whole are more aggressive in the later stages of the colony cycle when the nest is more valuable (Judd 1998).

The queen, as the primary egg layer (Metcalf & Whitt 1977), has the most direct reproductive investment in the nest and therefore, the most to lose. If the level of investment ultimately drives aggression in *P. fuscatus*, the queen's active participation in colony defence throughout the colony cycle would not be unexpected. The subordinate foundresses and workers have mostly indirect investment in the nest (Metcalf & Whitt 1977). For a subordinate individual, the amount of investment is positively correlated with the age of that individual. However, in the present study, the age of the colony did not correlate with the aggressiveness of the workers.

Younger workers were less aggressive than older workers, suggesting either the amount of investment is more important or the younger workers could potentially overwinter and start a colony the following year. Even the queen showed an increase in aggression over the colony cycle. The failure to see that change from Period 2 to Period 3 in the individual-level analysis may be due to a small working sample size, and more importantly that many of the queens were already at the maximum aggression level possible. Because dominance did not show any significant correlation with aggression and was not related to investment levels, one would not expect to find a relationship between aggression and dominance under the investment hypothesis. In fact I found no relationship between age and dominance. This result differs from the findings of West-Eberhard (1969).

Gynes and males completely abandoned the nest during an attack. Because they represent the embodiment of the reproductive investment of the colony, both the investment hypothesis and the reproductive options hypothesis would predict that they should not contribute to the nest's defence. At this stage of the colony cycle there was no brood, so defending the nest was unnecessary. The fact that the workers in Period 4 showed any aggression suggests they might be defending the reproductives. Interestingly, Gamboa et al. (1991) found that gynes will readily attack unrelated conspecifics on the nest. The authors suggested the gynes may be trying to prevent unrelated conspecifics from participating in nectar sharing, which occurs at this stage in the colony cycle.

The behaviour of *P. fuscatus* in response to a vertebrate predator is certainly not as straightforward as current models of social insects might predict (i.e. queens are not aggressive and the workers defend the colony). Whereas the subordinate foundresses and workers showed an increase in aggression with age as seen in other social insect colonies, the aggressive behaviour of the queens was quite different. A *Polistes* queen is faced with a work force that potentially has other options and behaves accordingly. Additionally, the queen has the most direct investment in the nest and stands to lose the most if the nest is destroyed. If investment and reproductive options hypotheses together drive aggressive behaviour in *P. fuscatus* queens, then we might expect to see queen aggression displayed in social insects with similar colony compositions. Otherwise, there may be additional factors in the life of *P. fuscatus* that cause this divergence from the stereotypical queen behaviour.

One possible factor that may affect queen aggression in *P. fuscatus* is the latitude in which these wasps are living. *Polistes fuscatus* live in a much more northern climate than most other *Polistes* in North America (*P. dominulus* has been introduced to the same climate; Judd & Carpenter 1996). This climate is characterized by a shorter warm period relative to the lower latitudes, and thus a shorter nesting period for *P. fuscatus*. Therefore, wasps in warmer climates have a longer safety window to renege if the original nest is destroyed. Tropical *Polistes* have a 6-month nesting period (Reeve 1990; Clapperton & Dymock 1997; Giannotti 1997), which is about 2 months longer than that of *P. fuscatus*. The tropical wasp

P. canadensis is reported to be able to start a new colony at any time during the year (Evans & West-Eberhard 1970). There may be a point at which the survival of the individual outweighs the survival of the nest. In the case of *P. fuscatus*, the survival of the nest may outweigh the survival of the queen when the nesting season is short. As the nesting season increases, and the safety window increases, the survival of the queen may outweigh the survival of the nest. This would predict that in *Polistes*, the aggressiveness of the queen towards a predator should increase as the nesting season decreases. Once more is learned about the defensive behaviour of other species of *Polistes* and other social insects against vertebrate predators we will have a better understanding of how aggression in *P. fuscatus* queens evolved.

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References

- Akre, R. D. & Reed, H. C. 1984. Vespine defense. In: *Defensive Mechanisms in Social Insects* (Ed. by H. R. Hermann), pp. 59–94. New York: Praeger.
- Aoki, S. 1987. Evolution of sterile soldiers in aphids. In: *Animal Societies: Theories and Facts* (Ed. by Y. Ito, J. L. Brown & J. Kikkawa), pp. 53–65. Tokyo: Japan Science Society Press.
- Bartz, S. H. 1979. Evolution of eusociality in termites. *Proceedings of the National Academy of Sciences, U.S.A.*, **76**, 5764–5768.
- Bourke, A. F. G. & Franks, N. R. 1995. *Social Evolution in Ants*. Princeton, New Jersey: Princeton University Press.
- Clapperton, B. K. & Dymock, J. J. 1997. Growth and survival of colonies of the Asian paper wasp, *Polistes chinensis antennalis* (Hymenoptera: Vespidae), in New Zealand. *New Zealand Journal of Zoology*, **24**, 9–15.
- Crespi, B. J. 1992. Eusociality in Australian gall thrips. *Nature*, **359**, 724–726.
- Dawkins, R. & Brockmann, H. J. 1980. Do digger wasps commit the Concorde fallacy? *Animal Behaviour*, **28**, 892–896.
- Dejean, A. & Lachaud, J. P. 1991. Polyethism in the ponerine ant *Odontomachus troglodytes*: interaction of age and interindividual variability. *Sociobiology*, **18**, 177–196.
- Evans, H. E. & West-Eberhard, M. J. 1970. *The Wasps*. Ann Arbor: University of Michigan Press.
- Fishwild, T. G. & Gamboa, G. J. 1992. Colony defense against conspecifics: caste-specific differences in kin recognition by paper wasps, *Polistes fuscatus*. *Animal Behaviour*, **43**, 95–102.

- Gamboa, G. J. & Stump, K. A. 1996. The timing of conflict and cooperation among cofoundresses of the social wasp *Polistes fuscatus* (Hymenoptera: Vespidae). *Canadian Journal of Zoology*, **74**, 70–74.
- Gamboa, G. J., Foster, R. L., Scope, J. A. & Bitterman, A. M. 1991. Effects of stage of colony cycle, context and intercolony distance on conspecific tolerance by paper wasps (*Polistes fuscatus*). *Behavioral Ecology and Sociobiology*, **29**, 87–94.
- Gamboa, G. J., Wacker, T. L., Duffy, K. G., Dobson, S. W. & Fishwild, T. G. 1992. Defence against intraspecific usurpation by paper wasp cofoundresses (*Polistes fuscatus*, Hymenoptera: Vespidae). *Canadian Journal of Zoology*, **70**, 2369–2372.
- Gerber, C., Badertscher, S. & Leuthold, R. H. 1988. Polyethism in *Macrotermes bellicosus* (Isoptera). *Insectes Sociaux*, **35**, 226–240.
- Giannotti, E. 1997. Biology of the wasp *Polistes* (*Epicnemius cinerascens* Saussure (Hymenoptera: Vespidae). *Anais Da Sociedade Entomologica do Brasil*, **26**, 61–67.
- Gibo, D. L. 1978. The selective advantage of foundress associations in *Polistes fuscatus* (Hymenoptera: Vespidae): a field study of the effects of predation on productivity. *Canadian Entomologist*, **110**, 519–540.
- Hölldobler, B. & Wilson, E. O. 1990. *The Ants*. Cambridge, Massachusetts: Belknap Press.
- Jeanne, R. L. 1982. Predation, defense, and colony size and cycle in social wasps. In: *The Biology of Social Insects* (Ed. by M. C. Breed, C. Michener & H. E. Evans), pp. 280–284. Boulder, Colorado: Westview Press.
- Jeanne, R. L. 1991. Polyethism. In: *The Social Biology of Wasps* (Ed. by K. C. Ross & R. W. Matthews), pp. 389–425. Ithaca, New York: Cornell University Press.
- Jeanne, R. L., Williams, N. M. & Yandell, B. S. 1992. Age polyethism and defense in a tropical social wasp (Hymenoptera: Vespidae). *Journal of Insect Behavior*, **5**, 211–227.
- Judd, T. M. 1998. Defensive behavior of colonies of the paper wasp, *Polistes fuscatus*, against vertebrate predators over the colony cycle. *Insectes Sociaux*, **45**, 1–12.
- Judd, T. M. & Carpenter, J. M. 1996. *Polistes dominulus* (Hymenoptera: Vespidae) found in Michigan. *Great Lakes Entomologist*, **29**, 45–46.
- Kurkut, G. A. & Gilbert, L. I. 1985. *Comprehensive Insect Physiology, Biochemistry and Pharmacology*. Vol. 5, *Nervous System: Structure and Motor Function*. Oxford: Pergamon Press.
- Lacey, E. A. & Sherman, P. W. 1991. Social organization of the naked mole-rat colonies: evidence for divisions of labor. In: *The Biology of the Naked Mole-rat* (Ed. by P. W. Sherman, J. U. M. Jarvis & R. D. Alexander), pp. 275–336. Princeton, New Jersey: Princeton University Press.
- Matthews, R. W. & Matthews, J. R. 1988. *Insect Behavior*. Malabar: Robert E. Krieger.
- Metcalfe, R. A. & Whitt, G. S. 1977. Intra-nest relatedness in the social wasp *Polistes metricus*. *Behavioral Ecology and Sociobiology*, **2**, 339–351.
- Michener, C. D. 1974. *The Social Behavior of Bees*. Cambridge, Massachusetts: Belknap Press.
- Noirot, C. 1989. Social structure in termite societies. *Ethology, Ecology and Evolution*, **1**, 1–17.
- Noonan, K. M. 1979. Individual strategies of inclusive-fitness-maximizing in foundresses of the social wasp, *Polistes fuscatus* (Hymenoptera: Vespidae). Ph.D. thesis, University of Michigan, Ann Arbor.
- O'Donnell, S. 1998. Effects of experimental forager removals on division of labour in the primitively eusocial wasp. *Behaviour*, **135**, 173–193.
- O'Donnell, S. & Jeanne, R. L. 1995. Implications of senescence patterns for the evolution of age polyethism in eusocial insects. *Behavioral Ecology*, **3**, 269–273.
- Oster, G. F. & Wilson, E. O. 1978. *Caste and Ecology in the Social Insects*. *Monographs in Population Biology*. Princeton, New Jersey: Princeton University Press.
- Owen, J. 1962. The behavior of the social wasp *Polistes fuscatus* (Vespidae) at the nest, with special reference to differences between individuals. Ph.D. thesis, University of Michigan, Ann Arbor.
- Page, R. E., Jr, Post, D. C. & Metcalfe, R. A. 1989. Satellite nests, early males, and plasticity of reproductive behavior in a paper wasp. *American Naturalist*, **134**, 731–748.
- Pardi, L. 1948. Dominance order in *Polistes* wasps. *Physiological Zoology*, **21**, 1–13.
- Post, D. C., Downing, H. A. & Jeanne, R. L. 1984. Alarm response by social wasps *Polistes exclamans* and *P. fuscatus* (Hymenoptera: Vespidae). *Journal of Chemical Ecology*, **10**, 1425–1433.
- Pratte, M. 1997. Recognition and social dominance in *Polistes* wasps. *Journal of Ethology*, **15**, 55–59.
- Reed, H. C. & Vinson, S. B. 1979. Nesting ecology of paper wasps (*Polistes*) in Texas urban area (Hymenoptera: Vespidae). *Journal of the Kansas Entomological Society*, **52**, 673–689.
- Reeve, H. K. 1991. *Polistes*. *The Social Biology of Wasps* (Ed. by K. C. Ross & R. W. Matthews), pp. 99–148. Ithaca, New York: Cornell University Press.
- Riech, R. M., Mielke, P. W., Jr & Hawksworth, F. G. 1990. Application of permutation techniques in analyzing spatial patterns. *USDA Forestry Service General Techniques Report*, **263**, 384–389.
- Riech, R. M., Mielke, P. W., Jr & Hawksworth, F. G. 1991. Spatial analysis of ponderosa pine trees infected with dwarf mistletoe. *Canadian Journal of Forest Research*, **21**, 1808–1815.
- Robinson, G. E. & Page, R. E., Jr. 1988. Genetic determination of guarding and undertaking in honey-bee colonies. *Nature*, **333**, 356–358.
- Robinson, G. E., Page, R. E., Jr & Huang, Z. Y. 1994. Temporal polyethism in social insects is a developmental process. *Animal Behaviour*, **48**, 467–469.
- Seeley, T. D. 1985. *Honeybee Ecology*. Princeton, New Jersey: Princeton University Press.
- Starr, C. K. 1985. Enabling mechanisms in the origin of sociality in the Hymenoptera: the sting's the thing. *Annals of the Entomological Society of America*, **78**, 836–840.
- Starr, C. K. 1990. Holding the fort: colony defense in some primitively social wasps. In: *Insect Defenses* (Ed. by D. L. Evans & J. O. Schmidt), pp. 421–461. Albany: State University of New York Press.
- Stern, D. L. & Foster, W. A. 1996. The evolution of sterile soldiers in aphids. *Biological Review*, **71**, 27–79.
- Strassmann, J. E. 1981. Parasitoids, predators, and group size in the paper wasp, *Polistes exclamans*. *Ecology*, **62**, 1225–1233.
- Turillazzi, S. 1984. Defensive mechanisms in *Polistes* wasps. In: *Defensive Mechanisms in Social Insects* (Ed. by H. R. Hermann), pp. 33–59. New York: Praeger.
- West-Eberhard, M. J. 1969. The social biology of polistine wasps. *Miscellaneous Publications of the Museum of Zoology of the University of Michigan*, **140**, 1–101.
- Wilson, E. O. 1971. *The Insect Societies*. Cambridge, Massachusetts: Belknap Press.
- Yamane, S. & Kawamichi, T. 1975. Bionomic comparison of *Polistes biglumis* (Hymenoptera: Vespidae) at two different localities in Hokkaido northern Japan with references to its probable adaptation to cold climate. *Kontyu*, **43**, 214–232.
- Yanega, D. 1988. Social plasticity and early-diapausing females in a primitively social bee. *Proceedings of the National Academy of Sciences, U.S.A.*, **85**, 4374–4377.