

**Research article**

**Defensive behavior of colonies of the paper wasp,  
*Polistes fuscatus*, against vertebrate predators over the  
colony cycle**

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**Summary**

A major threat to eusocial colonies is predation (Starr, 1990) since these colonies place their entire reproductive investment into a single nest (Hansell, 1996). The vertebrate predator is probably the most destructive type of predator in that it can remove the entire nest and thereby destroy all of the investment made by the colony.

In this study I considered how the paper wasp, *Polistes fuscatus*, changes its defensive behavior over the colony cycle. The colonies were presented with a model of an adult Red-winged Black-bird and a speaker that vibrated the comb. The simulated attack was designed to give each colony the same experience.

The colonies of *Polistes fuscatus* became more aggressive over the colony cycle. After the emergence of the gynes, the colony showed no aggression towards a vertebrate predator. The aggression levels of the colony were positively correlated with the number of reproductive-destined brood (but not worker-destined brood) in the nest. This suggests that the brood representing direct reproductive investment (reproductive brood) affects the level of defense in the colony and not the indirect reproductive investment (worker brood).

**Introduction**

The nest has played a central role in the life histories of many animals (Andersson, 1984). By having a nest, an individual is able to centralize the location of its brood, thus providing a more efficient way to care for its offspring. A major cost to having all of one's reproductive investment in one place is that anything destroying the nest, such as a predator, can eliminate an individual's ability to reproduce in that season (Starr, 1985; Kukuk et al., 1989; Starr, 1990). Therefore nesting species have evolved mechanisms for defending the nest from potential predators (Starr, 1990).

Since the defense of a nest is costly (Oster and Wilson, 1978), the level of defense exhibited by an animal should reflect its level of investment. Nesting vertebrates such as birds will defend or abandon their nests depending on the age of the brood

(Winkler, 1992). Similarly social insects can vary the number of soldiers as a function of the number of reproductives present in the nest (Oster and Wilson, 1978).

Annual social insect colonies, colonies in which only the reproductive females overwinter, differ from perennial colonies in that perennial colonies also have to maintain a work force capable of sustaining the colony through the rest of the year. Although both types of colonies have many individuals contributing to the defense of the colony, annual colonies, as a whole, could be predicted to behave similar to nesting vertebrates such as birds. As with vertebrates, the only concern of the colony is its reproductive output for that season. After the young leave, the nest itself is worthless. The level of defense made by the colony should directly reflect the level of reproductive investment represented by its nest.

*Polistes* is an excellent model system to investigate the changes in colony behavior over the colony cycle. *Polistes* colonies invest all their resources into a single nest (Hansell, 1996; Andersson, 1984; Evans, 1977) and over the course of a summer the amount invested in the nest by the colony increases. Although this is also true for perennial colonies, the investment patterns of *Polistes* colonies are not complicated by the needs of the colony for overwintering or future reproduction. Thus within-season investment for this species is synonymous with fundamental life history allocation.

During early spring, a foundress or set of foundresses, initiates a nest (Reeve, 1991). At this stage of the colony cycle there are only a few eggs in the nest, and therefore the reproductive investment represented by the nest is minimal. Queens first produce a brood of workers who in turn help raise the reproductives. In *Polistes* wasps these reproductives emerge in late summer and reside on the nest until they depart to go into diapause in early fall (West-Eberhard, 1969; Reeve, 1991). Once all of the males and gynes (reproductive females) emerge, however, the reproductive value (Fisher, 1930) of the nest itself drops to zero. The level of reproductive investment represented by the nest should reflect how a *Polistes* colony would respond to a serious threat to the nest, such as an attack by a vertebrate predator.

Vertebrate predators are an important source of mortality for *Polistes* colonies (Turillazzi, 1984; Starr, 1985). Mammals such as foxes (Yamane and Kawamichi, 1975) and rodents (Reed and Vinson, 1979) have been seen attacking and eating *Polistes* colonies. Birds such as the Red-winged Blackbird, the Baltimore Oriole, and the Cardinal have all been noted to attack *Polistes* colonies in North America (Gibo, 1978). A single attack from a vertebrate can completely destroy the colony, reducing its occupants' fitness to zero. Therefore, defense mechanisms against vertebrates have evolved (Starr, 1985; Hermann, 1984).

While a few studies on social wasps looked for a division of labor in the defense against a vertebrate predator (*Polybia occidentalis*: Jeanne, 1992; *Parachartergus fraternus*: Jeanne 1991; *Parachartergus colobopterus*: Strassmann et al., 1990, *Polistes fuscatus*: Fishwild, 1991, *Polistes fuscatus*: Judd, 1996), little information exists on changes in the defensive behavior of a colony over a colony cycle. In this study, I examined the response of *Polistes fuscatus* colonies to a simulated vertebrate predator. I used a consistent and repeatable simulated vertebrate stimulus in order to insure the same attack experience was provided to each colony throughout the colony cycle. Using this simulated vertebrate predator, I examined how the

overall aggressiveness of the colony changed throughout the colony cycle and related those responses to the colony's demography.

## Methods

### *Study sites*

Study Site 1 is located at Oakland University, Rochester, Michigan (USA) in a natural area on campus. Study Site 2 is located in Metamora, Michigan on private property at the northeast corner of Kile Road and Baldwin Road. The colonies at Site 2 were developmentally about a week behind those of the colonies at Site 1.

Both study sites consisted of an open field surrounded by trees. I set out nestboxes along the tree line facing the open field. Nestboxes were 15 cm × 12.5 cm × 11.25 cm, and were constructed of wood with a 1.27 cm<sup>2</sup> mesh wire screen in front so the wasps could get through but larger animals (such as birds) could not. The bottoms of the nestboxes were hinged so they could be opened allowing one to mark the wasps or examine the comb. The nestboxes were suspended by wire from a wooden cross piece bolted to a metal post. The posts were located 10 m apart. These nestboxes were readily colonized by foundresses and all data below were gathered from colonies in these nestboxes.

### *Procedures*

The wasps were marked for individual identification with Testors® model paint. A small dot of paint was applied to the thorax of the wasps using very thin paint brushes. The foundresses were marked at sunrise on 25 May (Site 1) and 8 June (Site 2) 1995. Workers were first marked for individual identification on 7–8 July (Site 1) and 13–14 July (Site 2), and again on 30–31 July (Site 1) and 2–3 August (Site 2). There was a total of 30 colonies nesting in nestboxes at both study sites. Of these colonies, 13 were single-foundress colonies and 17 were multiple foundress colonies.

Each colony was presented with the simulated vertebrate predator at four different periods of the colony cycle:

Period 1 – Pre-worker emergence: only foundresses were present.

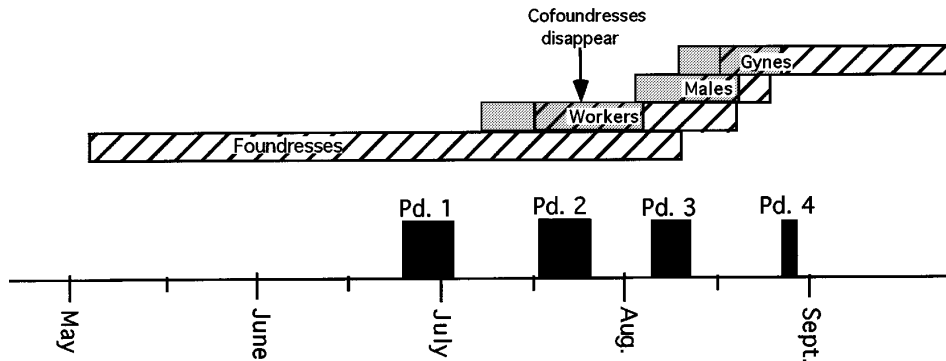
Period 2 – First worker emergence: approximately 5–7 days after the first workers emerged; all pupae were worker destined.

Period 3 – Late worker emergence: approximately 2–3 weeks after the first workers emerged; most pupae were reproductive destined.

Period 4 – Reproductive phase: predominantly reproductives were on the nest; few, if any, pupae left in the nest.

These phases, discussed in greater detail in Reeve (1991) and Judd (1996), are shown in Figure 1.

The simulated vertebrate predator consisted of both visual and vibrational stimuli, since wasps are highly sensitive to nest vibrations (Jeanne, 1982). The visual stimulus was a three dimensional, life sized, model of a male Red-winged Blackbird.



**Figure 1.** The colony cycle of *Polistes fuscatus*. The bars show the period of time each caste is found on the nest during the colony cycle (After Gamboa et al. 1991). The gray areas represent the presence of the pupae of that caste and the stripes indicate the presence of the adults of that caste. The ■ depicts the observation periods in which the colonies were presented with the simulated vertebrate predator

The bird model was made of black cloth with red wing markings and mounted on a stick. The vibrational stimulus was provided by a speaker (10 cm diameter, frequency response 55–5000 Hz, efficiency 84 dB, impedance 8 ohms) temporarily mounted on the nestbox by using two brass rods running through two eyelets that were screwed into the top of the nestbox. This allowed me to add or remove the speaker without disturbing the nests. A bass beat was played through the speaker at 160 beats per minute from a small cassette recorder that had a switch allowing me to operate the model and to control sound production.

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

While I conducted the simulation, the response of each individual on the nest to the simulated attack was recorded on audio tape and later transcribed. I attacked the colonies only once for each of the four time periods (Fig. 1) to minimize the possibility that the wasps would habituate to the simulation. There was at least a ten minute interval between presentations at different nests, minimizing any possible effects of an alarm pheromone on the model affecting wasps at the next colony (Post et al., 1984; Matthews and Matthews, 1988).

After the simulated attacks during periods 2 and 3, I counted the number of cells, eggs, larvae, and pupae in colony. The number of pupae was used as a measure of the reproductive value of the colony. At the pupal stage, the colony has completed all its investment into pupae short of defending them from predation. In Period 2, the brood is worker-destined, while in Period 3 the brood is reproductive-destined.

#### *Assays of aggression and data analysis*

The simulated attack elicited five different responses from the wasps. The responses were ranked subjectively in accordance with my impression of the level of aggres-

sion they represented. These behaviors have been categorized in a similar fashion by Starr (1990):

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

These behavioral responses were ranked from the least aggressive (1) to the most aggressive (5) response creating an Aggression Index (*AI*). They also reflected my impression of the levels of risk involved for an individual. Each wasp present during the simulated attack was assigned a numerical value of 1 to 5 based on its behavioral response to the simulated vertebrate attack and the median of all occupants was used to determine the *AI* of the colony.

The proportion of wasps (*PW*) coming off the nest aggressively was used as an additional assay to measure the level of aggression of a colony. This gave a measure of colony aggression that ranged from 0.0 to 1.0.

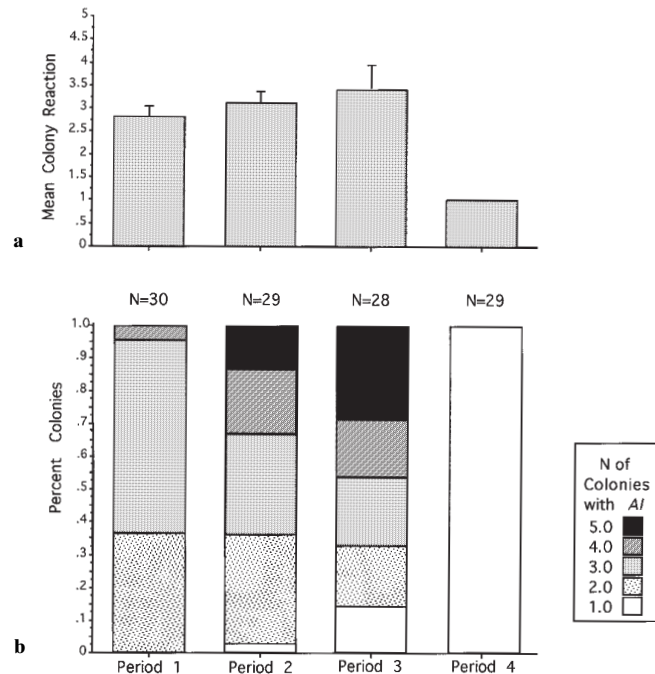
Unless noted otherwise, all correlations were done using the Spearman's Correlation and all inter-observation period analyses were done using the Friedman Test and Multiple Comparisons Procedure. Since there was no difference detected, data from both study sites ( $p > 0.05$ , Mann-Whitney U test) and data from multiple-foundress and single-foundress colonies ( $p > 0.05$ , Mann-Whitney U test) were combined. Changes in distributions were compared using the multi-response permutation procedure (MRPP)(Reich et al., 1990; Reich et al., 1991). The MRPP analysis allowed me to analyze the distributions without relying on the means. In this case the MRPP acted in the same fashion as a Chi Square contingency table but allowed me to use a smaller sample size (Reich et al., 1990).

## Results

The means of the colony aggression indices did not differ significantly among the first three observation periods, but decreased significantly in Period 4 to 1.0 ( $p = 0.005$ ; Fig. 2a). In Period 4, virtually all of the gynes flew away and did not defend their nest in response to a vertebrate predator. After completing the simulated attacks in Period 4, I looked among the branches of nearby trees and bushes and found the gynes sitting there. These gynes returned to the nest about an hour later.

When examining the distribution of aggression indices of the colonies (Fig. 2b), I noted that the distribution of *AI*'s changed over the colony cycle. These changes were found to be significant ( $p < 0.0001$ ; MRPP). Although the mean aggression indices did not change significantly over the first three periods (Fig. 2a), there was a significant change in the distribution of aggression indices in each observation period. I tested the distribution of *AI*'s across the first three periods with the MRPP procedure and this was significant as well ( $p < 0.0001$ ).

The proportion of wasps coming off the nest aggressively (*PW*) increased significantly from Period 1 to Period 2 and again from Period 2 to Period 3 ( $p = 0.0002$ ; Fig. 3). In Period 4 however the *PW*'s for all the nests dropped to almost 0.0.

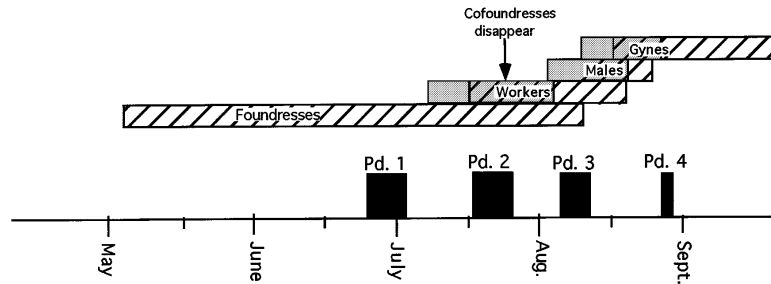


**Figure 2.** (a) The mean Aggression Indices (*AI*) of all of the colonies for the four observation periods. (b) Distribution of the Aggression Indices (*AI*) for the four observation periods

In Period 2 there was no significant correlation between the number of wasps on the comb and the aggression level of the colony (Table 1). Therefore, during the early stages of post-worker emergence (7–10 days after worker emergence), there was no evidence that the number of wasps on the nest was associated with the aggression level of the colony. However, in Period 3 there was a strong positive correlation between the number of wasps on the nests and the aggressive index of the colony ( $p=0.008$ , Table 1). In the final stages of post-worker emergence, the number of wasps present on the nest was positively associated with the aggressiveness of the colony.

#### *The relation between aggression and the number of pupae in the colony*

In Period 2, the *AI* of the colony (Table 1) and the proportion of wasps coming off the nest aggressively (Table 1) were not significantly correlated with the number of pupae in the nest. In Period 3, however, there was a significant positive correlation between the *AI* of the colony and the number of pupae in the nest ( $p=0.05$ ) as well as a significant positive correlation between the proportion of wasps coming off the nest aggressively and the number of pupae ( $p=0.008$ ). After a table wide sequential Bonferroni test (at  $\alpha = 0.05$ ; Rice, 1989) was performed on Table 1, the relationship between the colony *AI* and pupae number (Table 1) was found to be



**Figure 3.** Proportion of wasps coming off the nest aggressively (*PW*) for the colonies of *Polistes fuscatus* over the four observation periods. The values at each observation period are significantly different (Friedman's Test and the Multiple-Comparison Test Procedure)

**Table 1.** Correlations of the measures of colony aggressiveness (*AI*) and (*PW*) to the number of workers present and the number of pupae present on the nest during a simulated vertebrate attack. The table indicates the results of a Spearman's Correlation. The number of colonies is given in parentheses

	Period 2	Period 3
<i>AI</i> -Worker #	0.18 (11) p=0.34	0.51 (11) p=0.008*
<i>AI</i> -Pupae #	0.02 (22) p=0.92	0.50 (16) p=0.05
<i>PW</i> -Pupae #	0.29 (22) p=0.20	0.59 (16) p=0.008*

\* indicates values which are significant at  $\alpha = 0.05$  after a table wide sequential Bonferroni test was performed (Rice, 1989).

insignificant. Thus colony aggression of a colony and the number of pupae were strongly correlated when reproductive brood were present in the comb, but not when only worker brood were present.

**Discussion**

In many life history studies, the amount of reproductive investment plays a role in determining aggression. Vertebrate nesting species such as birds show an increase in aggression over a nesting period. Male birds are found to be increasingly more aggressive over the nesting cycle (Tree Swallows, Winkler, 1992; Willow Tit, Rytkönen, 1995; Eastern Kingbird, Siderius, 1994; Great Skuas, Hamer and Furness, 1993). Parents of the convict cichlid, *Cichlasoma nigrofasciatum*, also increase their level of defense with age of the young (Lavery, 1993). The level of investment will determine the level of defense the individuals are willing to take. The colonies of *P. fuscatus* in this study showed a similar pattern over the colony cycle. As the

colony cycle approached the emergence of the reproductives, the colonies became more aggressive (Fig. 2). The appearance of more colonies with *AI*'s of 1 in Period 3 could explain the lack of change in the mean *AI*. These may be colonies that have reached the final stages of colony development faster than other colonies. The increase in the percentage of aggressive colonies from periods 1 to 3, plus the increase in the *PW* of the colonies, suggests that the colonies are indeed becoming more aggressive from early to late in the summer. There was a sudden drop in aggression from Period 3 to Period 4 that was associated with gynes and males that fled the nest instead of staying to confront a vertebrate predator. At Period 4 of the colony cycle, the nest no longer contained any brood. In short, there was nothing left to defend so the most adaptive response appeared to be to abandon the nest and return later when the threat has passed.

The increase in the *PW* suggests that more individuals are participating in the defense of the colony against a vertebrate attack and at the same time some individuals are not participating in colony defense. This is consistent with the temporal polyethism in defensive behavior seen at the individual level (Judd, 1996).

Perhaps colonies with a greater number of individuals, are more aggressive as seen in some perennial colonies such as honey bees (Schneider and McNally, 1992). In perennial colonies that produce soldier castes, the larger colonies are able to produce more defenders than smaller colonies (Tschinkel, 1993). These colonies could withstand more individual fatalities and still be able to survive. In this study, I found that there was a correlation with size and aggressiveness of *P. fuscatus* colonies only in Period 3. However, colony size per se does not explain aggression at other times. In particular, Period 4 had the lowest aggression indices, although the greatest number of wasps were on the nest at this time. I ascribe this drop in aggression to the fact that *Polistes* colonies don't last for more than one season and don't have to invest in individuals to keep the colony alive during the winter.

Brood composition differed strongly between the observation periods. In Period 2, the brood was made up entirely of worker-destined larvae and pupae, whereas in Period 3, the larvae and pupae consisted of reproductive-destined brood. The lack of correlation between aggressiveness and pupal number in Period 2 and a strong correlation in Period 3 suggests that the colony changes its defensive response to vertebrate predators based primarily on the reproductive investment in the colony rather than on total investment (i.e., worker brood and reproductive brood). This is a marked difference from many birds which do not adjust their aggressiveness depending on the brood size (*Parus montanus*, Rytönen, 1995; *Falco tinnunculus*; Tolonen and Korpimäki, 1995; water fowl, Forbes et al., 1994; *Lagopus lagopus*, Martin and Horn, 1993; *Turdus pilaris*, Hogstad, 1992). However, a few studies suggest that certain fish (Coleman et al., 1985) and Redwinged Blackbirds (Robertson and Biermann, 1979) may increase their defense intensity with brood size. Goldfinches with larger broods will spend more time leading potential predators away from their nests (Knight and Temple, 1986). The fact that some birds show a relationship with brood size and some birds do not suggests that there might be a similar variation between different species of wasps as well.

Colonies with specialized soldiers such as the bamboo aphid *Pseudoregma bambucicola* (Sunose et al., 1991), the fire ant *Solenopsis invicta* (Tschinkel, 1993), and many species of termites (*Macrotermes michaelseni*: Darlington, 1986, *Cubitermes subcrenulatus*: Bodot, 1969, *Odontotermes redemanni*: Banerjee, 1966; Haverty, 1977, and *Cubitermes predorianus*: Ferrar, 1982) adjust the number of defenders during the colony cycle to coincide with reproduction. The soldier population increases as the colony approaches the production of alates and peaks just before these individuals disperse from the colony. After this, the production of soldiers dramatically decreases. Similarly, *P. fuscatus* colonies appeared to vary the number of individuals that defend the colony depending on how much has been invested into the production of the reproductives (Table 1). Strassmann et al. (1990) found that *Parachartergus colobopterus* did not attack when their nest was disturbed. They attributed this lack of aggression to the low levels of relatedness within a nest. It may have been related to the type of brood (either worker or reproductive brood) in the nest, although the exact time in the colony cycle the nest was attacked was not specified. Jeanne and Keeping (1995) found that *P. colobopterus* not only have an alarm signal but will spray their venom at an intruder attacking the nest. This suggests that *P. colobopterus* will show aggression towards an attacker during at least part of their colony cycle.

In my study, there were positive correlations between the number of reproductive brood and the aggressiveness of the *Polistes fuscatus* colony. *Polistes* has a life cycle where worker production is gradually replaced by the production of reproductives (Noonan, 1979; Reeve, 1991). The *Polistes fuscatus* colonies showed changes in aggression that reflected the level of reproductive investment represented by the nest. In advanced eusocial societies this temporally separated production of workers and reproductives is lost (Wilson, 1971). In addition, the chances of successfully reinitiating a nest also decreases. By the time the reproductive brood is in the comb there is very little chance of starting over if the nest is destroyed. This combined with the type of brood in the comb will enhance the reproductive value represented by the nest.

As we move across the social spectrum from species producing annual nests to producing perennial nests, colonies no longer produce a single reproductive brood but also produce subsequent broods as well. As a result, the direct correlation between investment and aggression is closely tied to the age and size of a colony and the amount of resources available to the colony. Perennial colonies are generally larger, longer lived, and have a more defined caste structure. These colonies only need to vary the proportion of defenders present in the nest. Perennial colonies would have to regulate their response based on the amount of resources available to them rather than the amount of reproductive brood they have (Oster and Wilson, 1978). Reproductive investment may have played an important role in shaping the behavioral structure of the colony in the initial stages of the development of eusociality. Once the colonies evolved into systems that produce more than one reproductive brood, the direct effects of reproductive investment on the response of a colony may have become less apparent and replaced by the direct effects of the age, size and resource availability.

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## References

- Andersson, M., 1984. The evolution of eusociality. *Ann. Rev. Ecol. and Syst.* 15:165–189.
- Banerjee, B., 1966. A statistical study of the population of tropical moundbuilding termite *Odontotermes redemanni* (Wasmann). *Insectes soc.* 13:29–38.
- Bodot, P., 1969. Composition des colonies de termites: ses fluctuations au cours du temps. *Insectes soc.* 16:39–54.
- Coleman, R.M., M. R. Gross and R. C. Sargent, 1985. Parental investment decision rules: a test in bluegill sunfish. *Behav. Ecol. Sociobiol.* 18:59–66.
- Darlington, J.P.E.C., 1986. Seasonality in mature nests of the termite *Macrotermes michaelsoni* in Kenya. *Insectes soc.* 33:168–189.
- Evans, H.E., 1977. Extrinsic versus intrinsic factors in the evolution of insect sociality. *Biosci.* 27:613–617.
- Ferrar, P., 1982. Termites of the South African savanna. II: densities and populations of smaller mounds, and seasonality of breeding. *Oecol.* 52:133–138.
- Fisher, R.A., 1930. *The General Theory of Natural Selection*. 2nd ed., 1958. New York. Dover.
- Fishwild, T.G., 1991. Division of Labor in Colony Defense by the Primitively Eusocial Paper Wasp, *Polistes fuscatus* (Hymenoptera: Vespidae). M. S. Thesis, Oakland University, Rochester, MI.
- Forbes, M.R.L., R.G. Clark, P.J. Weatherhead and T. Armstrong, 1994. Risk-taking by female ducks: Intra- and interspecific tests of nest defense theory. *Behav. Ecol. Sociobiol.* 34:79–85.
- Gamboa, G.J., R.L. Foster, J.A. Scope and A.M. Bitterman, 1991. Effects of stage of colony cycle, context, and intercolony distance on conspecific tolerance by paper wasps (*Polistes fuscatus*). *Behav. Ecol. Sociobiol.* 29:87–94.
- 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. *Can. Ent.* 110: 519–540.
- Hamer K. C. and R. W. Furness, 1993. Parental investment and brood defense by male and female Great Skuas *Catharacta skua* the influence of food supply, laying date, body size, and body condition. *J. Zool.* 230:7–18.
- Hansell, M.H., 1996. Wasps make nests: nests make conditions. In: *Natural History and Evolution of Paper-Wasps* (S. Turillazzi and M.J. West-Eberhard, Eds.), Oxford University Press, Oxford, pp. 272–289.
- Haverty, M.I., 1977. The proportion of termites in termite colonies: a list and a bibliography. *Sociobiol.* 2:199–216.
- Hermann, H.R., 1984. Defensive mechanisms: general considerations. In: *Defensive Mechanisms in Social Insects* (H.R. Hermann, Ed.), Praeger Publishers: New York, New York. pp. 1–31.
- Hogstad, O., 1992. The relationship between nest defense and clutch size in fieldfares, *Turdus pilaris*, a field experiment. *Fauna Norvegica Series C Cinclus.* 15:45–48.
- Jeanne, R.L., 1982. Predation, defense, and colony size and cycle in social wasps. In: *The Biology of Social Insects* (M.C. Breed, C.D. Michener and H.E. Evans, Eds.), Westview Press. Boulder, Colorado, pp. 280–284.
- Jeanne, R.L., 1991. Polyethism. In: *The Social Biology of Wasps* (K. C. Ross and R. W. Matthews, Eds.), Cornell University Press. Ithaca, New York. pp. 389–425.
- Jeanne, R.L., 1992. Age polyethism and defense in a tropical social wasp (Hymenoptera: Vespidae). *J. Ins. Behav.* 5:211–227.

- Jeanne, R.L. and M.G. Keeping, 1995. Venom spraying in *Parachartergus colobopterus*: a novel defensive behavior in a social wasp (Hymenoptera: Vespidae). *J. Ins. Behav.* 8: 433–442.
- Judd, T.M., 1996. The defensive behavior of colonies of the paper wasp *Polistes fuscatus* against a vertebrate predator. M.S. Thesis, Oakland University, Rochester, MI.
- Knight, R.L. and S.A. Temple, 1986. Nest defense in the American goldfinch. *Anim. Behav.* 34: 887–897.
- Kukuk, P.K., G.C. Eickwort, M. Raveret-Richter, B. Alexander, R. Gibson, R.A. Morse and F. Ratnieks, 1989. Importance of the sting in the evolution of sociality in the Hymenoptera. *Ann. Entom. Soc. Am.* 82:1–5.
- Lavery R.J., 1995. Changes in offspring vulnerability account for the increase in convict cichlid defensive behaviour with brood age: Evidence for the nest crypsis hypothesis. *Anim Behav.* 49:1177–1184.
- Martin K. and A.G. Horn, 1993. Clutch defense by male and female Willow Ptarmigan *Lagopus lagopus*. *Ornis Scandinavica* 24:261–266.
- Matthews, R.W. and J.R. Matthews, 1988. *Insect Behavior*. Robert E. Krieger Publishing Company, Malabar.
- Noonan K.M., 1979. Individual Strategies of Inclusive Fitness Maximizing in the Social Wasp, *Polistes fuscatus* (Hymenoptera: Vespidae). PhD dissertation, The University of Michigan, Ann Arbor, Michigan.
- Oster, G.F. and E.O. Wilson, 1978. *Caste and Ecology in the Social Insects. Monographs in Population Biology*. Princeton University Press, Princeton.
- Post, D.C., H.A. Downing and R.L. Jeanne, 1984. Alarm response by social wasps *Polistes exclamans* and *P. fuscatus* (Hymenoptera: Vespidae). *J. Chem. Ecol.* 10:1425–1433.
- Reed, H.C. and S.B. Vinson, 1979. Nesting ecology of paper wasps (*Polistes*) in Texas urban area (Hymenoptera: Vespidae). *J. Kansas Entom. Soc.* 52:673–689.
- Reeve, H.K., 1991. *Polistes*. In: *The social biology of wasps* (K.C. Ross and R.W. Matthews, Eds.), Cornell University Press. pp. 99–148.
- Reich, R.M., P.W. Mielke, Jr. and F.G. Hawksworth, 1990. Application of permutation techniques in analyzing spatial patterns. In: *State-of-the-Art Methodology of Forest Inventory: A Symposium Proceedings, 30 July–5 Aug. 1989*, Syracuse NY. USDA For. Serv. Gen. Tech. Rep. PNW-GTR-263. pp 384–389.
- Reich, R.M., P.W. Mielke, Jr. and F.G. Hawksworth, 1991. Spatial analysis of ponderosa pine trees infected with dwarf mistletoe. *Can. J. For. Res.* 12:1808–1815.
- Rice, W.R., 1989. Analyzing Tables of Statistical Tests. *Evol.* 43:223–225.
- Robertson, R.J. and G.C. Biermann, 1979. Parental investment strategies determined by expected benefits. *Z. Tierpsychol.* 50:124–128.
- Rytkönen, S., 1995. Parental care in the willow tit (*Parus montanus*): Nest defense and nestling provisioning in the light of the parental investment theory. *Acta Universitatis Ouluensis Series a Scientiae Rerum Naturalium.* (265):1–37.
- Schneider, S.S. and L.C. McNally, 1992. Colony defense in the African honey bee in Africa (Hymenoptera: Apidae). *Environ. Entom.* 21:1362–1370.
- Siderius, J.A., 1993. Nest defense in relation to nesting stage and response of parents to repeated model presentations in the eastern kingbird (*Tyrannus tyrannus*). *Auk* 110:921–923.
- Starr, C.K., 1985. Enabling mechanisms in the origin of sociality in the Hymenoptera – The sting's the thing. *Ann. Entom. Soc. Am.* 78:836–840.
- Starr, C.K., 1990. Holding the fort: colony defense in some primitively social wasps. In: *Insect defenses* (D.L. Evans and J.O. Schmidt, Eds.), State University of New York Press, Albany. pp. 421–461.
- Strassmann, J.E., C.R. Hughes and D.C. Queller, 1990. Colony defense in the social wasp, *Parachartergus colobopterus*. *Biotropica.* 22:324–327.
- Sunose, T., S. Yamane, K. Tsuda and K. Takasu, 1991. What do the soldiers of *Pseudoregma bambucicola* (Homoptera, Aphidoidea) defend? *Japan. J. Entom.* 59:141–148.
- Tolonen, P. and E. Korpimäki, 1995. Parental efforts of kestrels (*Falco tinnunculus*) in nest defense: effects of lying time, brood size, and varying survival prospects of offspring. *Behav. Ecol.* 6:435–441.

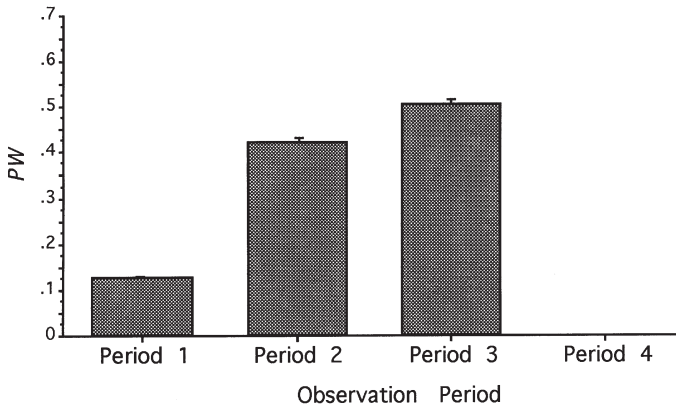
- Tschinkel, W.R., 1993. Sociometry and sociogenesis of colonies of the fire ant *Solenopsis invicta* during one annual cycle. *Ecol. Mono.* 63:425–457.
- Turillazzi, S., 1984. Defensive mechanisms in *Polistes* wasps. In: *Defensive Mechanisms in Social Insects*. (H.R. Hermann, Ed.), Praeger Publishers: New York, New York. pp. 33–94.
- 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*. The Belknap Press of Harvard University Press: Cambridge, Mass.
- Winkler, D.W., 1992. Causes and consequences of variation in parental defense behavior by tree swallows. *Condor*. 94:502–520.
- Yamane, S. and T. Kawamichi, 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, Tokyo*. 43:214–232.

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## Erratum

Judd, T. M., 1998. Defensive behavior of colonies of the paper wasp, *Polistes fuscatus*, against vertebrate predators over the colony cycle. *Insectes soc.* 45: 197–208.

Due to an unfortunate error, the article by T.M. Judd in the previous issue Vol. 45/2 appeared with a wrong version of Figure 3 on page 203. We here print the correct Figure 3 of this article. The Editor and Publisher very much apologize for this error.



**Figure 3.** Proportion of wasps coming off the nest aggressively (*PW*) for the colonies of *Polistes fuscatus* over the four observation periods. The values at each observation period are significantly different (Friedman's Test and the Multiple-Comparison Test Procedure)