The Great Lakes Entomologist

Volume 36
Number 3 & 4 - Fall/Winter 2003 *Number 3 & 4 - Fall/Winter 2003*

Article 1

October 2003

Behavioral Differences Between Two Recently Sympatric Paper Wasps, the Native *Polistes Fuscatus* and the Invasive *Polistes Dominulus*

Stephanie A. Silagi
Oakland University

George J. Gamboa
Oakland University

Carrie R. Klein
Oakland University

Melissa A. Noble
Oakland University

BEHAVIORAL DIFFERENCES BETWEEN TWO RECENTLY SYMPATRIC PAPER WASPS, THE NATIVE *POLISTES FUSCATUS* AND THE INVASIVE *POLISTES DOMINULUS*

Stephanie A. Silagi[1] , George J. Gamboa[1], Carrie R. Klein[1] and Melissa A. Noble[1]

ABSTRACT

Polistes dominulus (Christ), an old world paper wasp, was introduced into the eastern United States in the 1970s and has been rapidly spreading westward. Recently, it has displaced the native *Polistes fuscatus* (F.) in at least some areas of Michigan. In order to understand why *P. dominulus* has been so successful, several behavioral attributes were compared between *P. dominulus* and *P. fuscatus* at a Michigan field site that contained colonies of both species nesting semi-naturally in plywood nestboxes.

Preworker colonies of *P. dominulus* had a significantly greater tendency to store nectar (and had significantly higher proportions of cells with nectar) than preworker colonies of *P. fuscatus*. This finding may explain the higher survivorship of *P. dominulus* foundresses reported in a previous study. *P. dominulus* also had a significantly greater tendency to build vertical nests and had significantly more pedicels per comb and per cell than *P. fuscatus*. These findings suggest that compared to *P. fuscatus, P. dominulus* may have more flexibility in the positioning of its combs and, because of a possibly stronger attachment of the comb to a substrate, may be less susceptible to bird predation. The higher winter survivorship reported for *P. fuscatus* over *P. dominulus* in a previous study does not appear to be due to differences in the proportions of gynes stranded on their nests late in the fall. Finally, behavioral evidence from videography was consistent with previous reports that *P. dominulus* is not replacing *P. fuscatus* through direct agonistic interactions.

The invasive European paper wasp, *Polistes dominulus* (Christ), has been spreading rapidly westward since its introduction to the Boston area in the late 1970s (Pickett and Wenzel 2000; Gamboa et al. 2002). *Polistes dominulus* was first reported in Michigan in 1995 (Judd and Carpenter 1996) and, in at least some areas of Michigan, has completely replaced the only native paper wasp, *P. fuscatus* (F.) (Gamboa et al. 2002).

Pickett and Wenzel (2000) and Gamboa et al. (2002) documented that colonies of *P. dominulus* are much more productive than colonies of the native *P. metricus* Say and *P. fuscatus* in Ohio and Michigan, respectively. Gamboa et al. (2002) reported that *P. dominulus* had a number of potential advantages over *P. fuscatus* that likely contributed to its higher productivity. These advantages included earlier production of workers and greater per capita foraging rates. Interestingly, Gamboa et al. (2002) found no evidence that *P. dominulus* was negatively affecting *P. fuscatus* directly through agonistic encounters.

Gamboa et al. (2002) reported that foundresses of *P. dominulus* also had significantly higher survivorship than foundresses of *P. fuscatus*. In our present study, we examined nectar storage in the two species to determine if the enhanced survivorship of *P. dominulus* might be due to greater nectar stores. We also compared the positioning of the nest and the number of pedicels in nests to

[1]Department of Biological Sciences, Oakland University, Rochester, MI 48309.

determine if *P. dominulus* might have greater flexibility in its choice of nest sites and a stronger attachment of the comb to the substrate than *P. fuscatus*. Gamboa et al. (2004) found that *P. dominulus* had a significantly lower survivorship during winter diapause than *P. fuscatus*. We compared the number of gynes stranded on late fall nests in the two species to determine if this might explain their differential winter survivorship. Finally, we observed behavioral interactions between *P. fuscatus* and *P. dominulus* foundresses that had nested together naturally in field nestboxes.

METHODS

To compare nectar storage in *P. fuscatus* and *P. dominulus*, on 14 May 2002 we surveyed 90 plywood nestboxes of which 76 contained preworker colonies (36 *P. fuscatus* and 40 *P. dominulus*) at the Oakland University Preserve (located 50 km north of Detroit, Michigan). For a description of nestboxes and the field site, see Judd (1998). During the survey we recorded the presence or absence of nectar in each comb. In 2003, we surveyed 90 nestboxes of which 72 contained colonies (31 *P. fuscatus* and 41 *P. dominulus*) prior to the first emergence of workers on 27 June and again after first worker emergence on 13 July. For each colony surveyed on 27 June and 13 July in 2003, we recorded the number of foundresses, the number of cells in the comb, and the number of cells that contained nectar. For both 2002 and 2003, foundresses were marked in mid-May with Testors enamel (The Testor Corporation, Rockford, IL.) for individual identification.

We recorded the positions of combs in nestboxes containing colonies in surveys of 76 nestboxes on 7 May 2002 and 72 nestboxes on 2 June 2003. For each survey, we recorded the number of foundresses, the number of cells in the comb, and whether the comb was attached to the top of the nestbox (horizontal surface) or the back of the nestbox (vertical surface). For 2003 colonies, we collected and counted the gynes on each comb in early November after which temperatures remained below critical flight temperatures (~15° C) for the remainder of the year. These gynes were stranded on their nests and unable to fly to protected hibernaculae to spend the winter. In December after the completion of the colony cycle in 2002 and 2003, we removed combs from nestboxes and counted the number of cells and pedicels in each comb.

We conducted videography of four preworker colonies that nested naturally in two nestboxes (12 h total) to observe behavioral interactions between foundresses of *P. fuscatus* and *P. dominulus*. In 2001, we videotaped four, two-hour segments (on 8, 9, 10 and 18 May) of a nestbox that contained a single-foundress colony of *P. fuscatus* and a single-foundress colony of *P. dominulus*. In 2003, we videotaped two, two-hour segments (on 28 and 29 May) of a nestbox that contained a single-foundress colony of *P. fuscatus* and a single-foundress colony of *P. dominulus*. In both 2001 and 2003, the heterospecific combs in each nestbox were approximately 5 – 6 cm apart. Videotapes were viewed in the laboratory by one observer and the numbers and kinds of interactions between heterospecific foundresses, as well as the initiator of each interaction, were recorded.

Whenever we had adequate sample sizes of matched colonies, we utilized matched comparisons for data analyses. Interspecific matched comparisons involved a colony of *P. dominulus* and a spatially proximate (< 10m apart) colony of *P. fuscatus* with the same number of foundresses. Intraspecific matched comparisons involved a single-foundress colony and a spatially proximate (<10m apart) multiple-foundress colony of the same species. Matched colonies, which had presumably experienced similar environmental conditions (insolation, temperatures, etc.), were compared statistically with Wilcoxon Matched-Pairs tests (Siegel and Castellan 1988). Means are followed by standard deviations. All statistical tests are two-tailed.

RESULTS

Preworker *P. dominulus* colonies were significantly more likely to have nectar stored in their combs than colonies of *P. fuscatus*. Of 148 single- and multiple-foundress colonies surveyed in 2002 and 2003, 68 of 84 (81%) *P. dominulus* nests but only 38 of 64 (59%) *P. fuscatus* nests contained stored nectar ($P < 0.02$, Chi-Square test). *Polistes dominulus* colonies also had significantly more cells containing nectar (mean = 10.9) than did colonies of *P. fuscatus* (mean = 3.9, $P = 0.005$, Table 1). Since *P. dominulus* colonies are larger than *P. fuscatus* colonies (Gamboa et al. 2002), it may be that the greater number of cells containing nectar in *P. dominulus* is simply a reflection of their greater number of cells. This was not the case. *Polistes dominulus* colonies had a significantly higher percentage of their total cells containing nectar (mean = 13.3%) than did *P. fuscatus* colonies (mean = 4.6%, $P = 0.001$, Table 1).

In preworker surveys, multiple-foundress colonies of both species had a greater percentage of their cells with nectar than did single-foundress colonies, but the differences were not significant. For *P. fuscatus*, the percentage of cells that contained nectar for multiple- and single-foundress colonies was 6.2 (± 4.0) and 2.3 (± 3.2), respectively ($P = 0.08$, N = 9 matched pairs). For *P. dominulus*, the percentage of cells containing nectar for multiple- and single-foundress colonies was 16.8 (± 17.6) and 12.6 (± 9.5), respectively ($P = 0.45$, N = 13 matched pairs).

Postworker colonies of both species stored relatively little nectar in their combs. In 2003, only 9 of 31 (29 %) *P. fuscatus* colonies and 21 of 41 (51%) *P. dominulus* colonies contained nectar in their combs. The greater tendency of *P. dominulus* colonies to store nectar in postworker colonies was not significant ($P > 0.1$, Chi-Square test). Although *P. fuscatus* and *P. dominulus* postworker colonies did differ significantly in the number of cells with nectar ($mean_s = 0.07 \pm 0.26$ and 1.4 ± 2.7, respectively; $P < 0.04$), they did not differ in the proportion of cells with nectar ($mean_s = 0.7 \pm 0.5$ and 0.8 ± 0.9, respectively; $P > 0.3$, N = 16 matched pairs for both comparisons).

Of 148 nests constructed in 2002 and 2003, 15 were vertical nests and 133 were horizontal nests. Of the 15 vertical nests, 14 (7 single- and 7 multiple-foundress colonies) were constructed by *P. dominulus*. As a result, *P. dominulus* had a significantly greater tendency to build vertical nests than *P. fuscatus* ($P < 0.05$, Chi-Square test). Of the 14 *P. dominulus* vertical nests, 7 eventually expanded to the roof of the nestbox so that they occupied both the horizontal and vertical sides of the nestbox. For *P. dominulus*, the mean numbers of cells for vertical nests (mean = 243 ± 119) and horizontal nests (mean = 219 ± 108) were not significantly different ($P = 0.37$, N = 11 matched pairs).

Combs of *P. dominulus* had significantly more pedicels (mean = 7.72) than combs of *P. fuscatus* (mean = 2.07, $P = 0.0008$, Table 2). Furthermore, combs of *P. dominulus* had significantly more pedicels per cell than combs of *P. fuscatus* ($P = 0.04$, Table 2).

Table 1. Comparisons of nectar storage in preworker combs of *P. fuscatus* and *P. dominulus*.

Nectar Storage	*P. fuscatus*	*P. dominulus*	*P*[a]
Mean (± SD) No. of cells with nectar	3.9 ± 5.1	10.9 ± 8.8	0.005
Mean (± SD) % of cells with nectar	4.6 ± 4.9	13.3 ± 6.9	0.001

[a] N = 16 matched pairs of colonies.

Table 2. Comparisons of the number of pedicels in combs of *P. fuscatus* and *P. dominulus*.

Pedicel Number	***P. fuscatus***	***P. dominulus***	***P***
Mean (± SD) No. of pedicels/comb	2.07 ± 1.5	7.72 ± 8.3	0.0008[a]
Mean (± SD) No. of pedicels/cell	0.019 ± 0.012	0.026 ± 0.12	0.04[b]

[a] Mann-Whitney test, N = 29 and 46 colonies, respectively.
[b] N = 11 matched pairs of colonies.

There were significantly more gynes ($P = 0.016$) on *P. dominulus* combs than on *P. fuscatus* combs when gynes were collected in early November 2003. The mean numbers of gynes on *P. dominulus* and *P. fuscatus* combs were 3.8 ± 5.8 (N = 36 colonies) and 1.0 ± 1.9 (N = 29 colonies), respectively. However, when the numbers of gynes on combs were adjusted for the size of the comb, i.e., the number of cells, the difference between the two species was not significant ($P =$ 0.78, N = 11 matched pairs).

We recorded 19 interactions between heterospecific foundresses in 12 h of videography. All 19 interactions were initiated by the *P. fuscatus* foundress and consisted of her flying or walking to the comb of the *P. dominulus* foundress. In 12 of the 19 intrusions, the *P. dominulus* foundress successfully repelled the *P. fuscatus* foundress with lunges and/or biting. In 7 of the 19 intrusions, the *P. dominulus* foundress was temporarily chased from her nest. None of the four colonies produced adult offspring although the two *P. fuscatus* foundresses persisted longer on their nests in subsequent surveys than did *P. dominulus* foundresses.

DISCUSSION

Since combs of *P. dominulus* are more likely to contain nectar (and have larger stores of nectar) than combs of *P. fuscatus*, *P. dominulus* enjoys a potential advantage over its native congener during times when climatic conditions prevent foraging. In the preworker phase of the colony cycle, it is not uncommon for extensive periods of cool weather and rain to prevent foraging for several days or longer. One would assume that during such periods it would be advantageous for wasps trapped on their nest to have access to nectar stores. In addition to enhancing the well being of foundresses, nectar consumption at the nest might permit wasps to forage for colony needs (wood fibers and insect prey) rather than their own needs (nectar) immediately after favorable foraging conditions return.

Our results indicate that *P. dominulus* is more flexible in the positioning of its nest than *P. fuscatus*. This could be an advantage in cavity nesting when a suitable horizontal surface for the attachment of the comb is not present. Such flexibility may also allow *P. dominulus* to build larger nests by taking advantage of both horizontal and vertical surfaces in a cavity. Thus, *P. dominulus* may be more opportunistic than *P. fuscatus* in taking advantage of more diverse nesting situations. Armstrong and Stamp (2003) recently provided evidence that *P. dominulus* is more opportunistic than *P. fuscatus* with respect to prey foraging.

Birds are important nest predators of *Polistes* wasps. Various species of birds have been reported to knock nests to the ground and then consume the contents of the cells (Rau 1941, Gibo 1978, Noonan 1979). Our finding that *P. dominulus* combs have significantly more pedicels per comb and per cell suggests that combs of *P. dominulus* might be more securely attached to the substrate and more difficult to dislodge by avian predators than combs of *P. fuscatus*. In support of this hypothesis, we found that combs of *P. dominulus* were more difficult to remove from nestboxes than combs of *P. fuscatus*. Our survey data from previous years are also consistent with this hypothesis. In 1996 there were 23 colonies of *P. fuscatus*, but no colonies of *P. dominulus*, nesting on the eaves of a large building located adjacent to our field site. In 2000, there were 27 colonies of *P. dominulus*, but no *P. fuscatus* colonies, nesting on the same building. Thus, *P. dominulus* had completely replaced *P. fuscatus* on the building in a span of five years. In fact, *P. dominulus* had completely replaced *P. fuscatus* on all buildings of the university campus within this five-year period.

The complete replacement of *P. fuscatus* on the eaves of buildings contrasted with the persistence of *P. fuscatus* in nestboxes. In 2000, 33 of 46 colonies in nestboxes, which had wire screens to exclude vertebrate predators, were *P. fuscatus* colonies even though *P. dominulus* had begun nesting in nestboxes at our field site in 1995. The fact that colonies of *P. fuscatus* on all university buildings were completely replaced by *P. dominulus* within the same five year period (but the colonies in the nestboxes were not) suggests that birds may have been more successful in dislodging the combs of *P. fuscatus* than *P. dominulus* from the eaves of buildings. *P. dominulus* may also be more successful in renesting after avian nest predation. Gamboa et al. (2004) recently reported that *P. dominulus* was significantly more likely to successfully renest after raccoon predation than *P. fuscatus*.

It has been our experience over the past 23 years that gynes do not survive the winter in nestboxes at our field site. In previous years, paint-marked gynes who failed to leave their fall nests were found dead in their natal nestboxes the following spring. Thus, gynes remaining on their combs late in the fall after temperatures no longer permit flight probably perish.

Polistes dominulus has been reported to experience lower survivorship than *P. fuscatus* during winter diapause (Gamboa et al. 2004). Our results indicate that this difference in winter survivorship is probably not due to larger proportions of *P. dominulus* gynes being stranded on their fall natal nests.

Finally, our videography of heterospecific interactions is consistent with the evidence of Gamboa et al. (2002) that *P. dominulus* is not replacing *P. fuscatus* through direct agonistic encounters. Although our sample sizes are small, *P. fuscatus* was the initiator and aggressor in all of its interactions with *P. dominulus*. In a related finding, Gamboa et al. (2004) documented that the vast majority of attempted usurpations of both *P. fuscatus* and *P. dominulus* colonies were by foundresses of *P. fuscatus*. Therefore, *P. dominulus* appears to be displacing *P. fuscatus* through exploitative (indirect) competition in Michigan rather than interference (direct) competition.

ACKNOWLEDGMENTS

S. Silagi was partially supported by the Oakland University Undergraduate Scholarship in Ecology and Behavior. M. Noble was partially supported by an undergraduate research award from the Merck Foundation.

LITERATURE CITED

Armstrong, T. R. and N. E. Stamp. 2003. Colony productivity and foundress behaviour of a native wasp versus an invasive social wasp. Ecol. Entomol. 28: 635-644.

Gamboa, G. J., E. I. Greig and M. C. Thom. 2002. The comparative biology of two sympatric paper wasps, the native *Polistes fuscatus* and the invasive *Polistes dominulus* (Hymenoptera, Vespidae). Insect. Soc. 49: 45-49.

Gamboa, G. J., M. A. Noble, M. C. Thom, J. L. Togal, R. Srinivasan and B. D. Murphy. 2004. The comparative biology of two sympatric paper wasps in Michigan, the native *Polistes fuscatus* and the invasive *Polistes dominulus* (Hymenoptera, Vespidae). Insect. Soc. 51: 153-157.

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. Entomol. 110: 519-540.

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

Judd, T. M. and J. M. Carpenter. 1996. *Polistes dominulus* (Hymenoptera: Vespidae) found in Michigan. Great Lakes Entomol. 29: 45- 46.

Noonan, K. M. 1979. Individual strategies of inclusive fitness maximizing in the social wasp *Polistes fuscatus* (Hymenoptera: Vespidae). Ph. D. thesis, University of Michigan.

Pickett, K. M. and J. W. Wenzel. 2000. High productivity in haplometrotic colonies of the introduced paper wasp *Polistes dominulus* (Hymenoptera: Vespidae; Polistinae). J. New York Entomol. Soc. 108: 314-325.

Rau, P. 1941. Birds as enemies of *Polistes* wasps. Can. Entomol. 73: 196.

Siegel, S. and N. J. Castellan, Jr. 1988. Nonparametric Satatistics for the Behavioral Sciences (2nd ed.). McGraw-Hill, Inc. New York. 399 pp.