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EFFECTS OF DIFFERENT HABITATS ON THE PRODUCTIVITY OF THE NATIVE PAPER WASP *POLISTES FUSCATUS* AND THE INVASIVE, EXOTIC PAPER WASP *P. DOMINULUS* (HYMENOPTERA: VESPIDAE)

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ABSTRACT

We examined the colony productivities of the native paper wasp, *Polistes fuscatus* (Fab.),(Hymenoptera: Vespidae), and the invasive, exotic paper wasp, *P. dominulus* (Christ), in oak forest, oak forest-old field ecotone, and old field habitats at the Oakland University Preserve in Rochester, Michigan from 2003 to 2005. Both species of paper wasps exhibited significant differences in colony productivity among the three habitats. Generally, colonies were the most productive in the old field habitat and the least productive in the oak forest habitat.

Colonies of *P. dominulus* were significantly more productive than comparable colonies of *P. fuscatus* in all three habitats. There was no evidence that *P. fuscatus* was more competitive with *P. dominulus* in any of the three habitats. Thus, our results do not support the suggestion of Gamboa et al. (2004) and Liebert et al. (2006) that *P. fuscatus* may be more competitive with *P. dominulus* in less disturbed or forest habitats than in urban and rural habitats.

The invasive, European paper wasp, *Polistes dominulus* (Christ) (Hymenoptera: Vespidae), was first reported in the United States in 1978 (Eickwort 1978) and in Michigan in 1995 (Judd and Carpenter 1996). Since its introduction, *P. dominulus* has rapidly replaced the only native species of paper wasp, *Polistes fuscatus* (F.), in many urban and rural areas of southeastern Michigan (Gamboa et al. 2002). *P. dominulus* also appears to be at least partially supplanting *P. fuscatus* in Massachusetts (A. Liebert, pers. comm.), New York (E. Tibbetts and N. Stamps, pers. comm.), and southern Ontario, Canada (G. Otis, pers. comm.). *P. dominulus* is thought to be supplanting *P. fuscatus* by indirect (exploitative) competition although the critical resources in this competition are unknown (Gamboa et al. 2004). Gamboa et al. (2004) speculated that the two species may be competing for nest sites.

Polistes dominulus is much more productive than *P. fuscatus* in urban habitats: both single- and multiple-foundress colonies of *P. dominulus* are significantly larger than comparable colonies of *P. fuscatus* (Gamboa et al. 2004). A major factor that contributes to the high productivity of *P. dominulus* is its short larval and pupal stadia, which enables it to produce its first workers significantly earlier than *P. fuscatus*. *P. dominulus* enjoys other advantages over *P. fuscatus* including higher per capita foraging rates, greater survivorship, lower rates of parasitism by Strepsiptera, and lower conspecific usurpation pressures (Gamboa et al. 2004).

Although *P. dominulus* appears to be replacing *P. fuscatus* in many urban and rural areas, it's unknown whether *P. dominulus* will completely displace *P. fuscatus* throughout its range. Gamboa et al. (2004) and Liebert et al. (2006) suggested that *P. fuscatus* may persist in certain habitats in which it might be more competitive with *P. dominulus*. For example, *P. fuscatus* may be more competitive with *P. dominulus* in less disturbed or forest habitats than in urban and rural areas. Liebert et al. (2006) also suggested that *P. fuscatus* could persist in the northern regions of its range if it was better able to tolerate colder

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temperatures during winter diapause than *P. dominulus*. There is presently, however, no evidence to support these suggestions.

We designed our study to answer two questions. First, does habitat type affect productivity in *P. fuscatus* and *P. dominulus*? Second, if there are productivity differences among different habitats in the two species, is there evidence that *P. fuscatus* is more competitive with *P. dominulus* in a particular habitat? The latter question bears directly on the question of whether *P. fuscatus* will be completely replaced by *P. dominulus*.

METHODS

Our study was conducted in 2003, 2004, and 2005 at the Oakland University Preserve in Rochester, Michigan. The Preserve, which contains approximately 110 acres, consists primarily of a forest dominated by white, red, and black oak trees (Larch and Sakai 1985). These overstory trees have a mean age of approximately 125 years, and thus large areas of the Preserve have been undisturbed for extensive periods of time (Larch and Sakai 1985). The Preserve also contains several small (<5 acres) old fields, which consist primarily of grasses (Poaceae), weedy, shade-intolerant woody plants, and various wildflowers (Larch and Sakai 1985).

Plywood wasp nestboxes (Judd 1988) were first placed at the Preserve in 1981, and *Polistes* spp. have annually occupied the nestboxes since then. Both *P. dominulus* and *P. fuscatus* commonly nest in cavities such as pipes, electrical boxes, bird boxes, mailboxes, etc., which are nest sites similar to our plywood nestboxes. Nestboxes are located in three different habitats: the oak forest, the interface between the forest and old fields (ecotone), and the old fields. Nestboxes in the forest receive no direct sun, nestboxes in the ecotone receive either morning or afternoon sun, and nestboxes in the old fields receive both morning and afternoon sun. Forest and old field nestboxes were located from 10 – 40 m into the forest and 10 – 50 m into old fields, respectively. Ecotone nestboxes were in the old fields within 2 m of the forest edge.

Foundresses of *P. fuscatus* and *P. dominulus* initiated colonies in the nestboxes in mid- to late April. All foundresses were marked with Testors enamels (Testors Corp.) for individual identification about three weeks after nest initiation. We surveyed nestboxes weekly throughout the preworker phase of the colony cycle and every two to three weeks during the postworker phase of the colony cycle. During surveys, we recorded the species, number, and identities of foundresses in each nestbox. After the end of the colony cycle when combs no longer contained adults, we brought the nestboxes into a laboratory, removed the combs from the nestboxes, and counted the number of cells and the number of cells with meconia in each comb as an estimate of colony productivity. The number of cells and the number of meconial cells, both of which are highly positively correlated with the number of adults in a colony, have been commonly used as estimates of colony productivity in *Polistes* (Gamboa et al. 2002, 2004).

In 2003, 2004, and 2005, there were 84 (35 *P. fuscatus*, 49 *P. dominulus*), 91 (47 *P. fuscatus*, 44 *P. dominulus*), and 81 (33 *P. fuscatus*, 48 *P. dominulus*) colonies, respectively, in the nestboxes. In the late summers of 2002 and 2003, we removed about a third and half of the *P. dominulus* colonies, respectively, from the Preserve because we were concerned that we were losing our population of *P. fuscatus* (see Liebert et al. 2006). In order to minimize uncontrolled variables that might affect colony productivity, we used the following matched comparisons for statistical analyses. To determine if habitat types affect productivity, we compared the productivity of a forest colony with the nearest conspecific ecotone colony and nearest conspecific old field colony that had the same number of foundresses. To determine if the relative productivities of *P. fuscatus* and *P. dominulus* differed among the three habitat types, we compared the productivity of a *P. fuscatus* colony with the nearest colony of *P. dominulus* that was in the same habitat and had the same number of foundresses. Our use of matched data sets controlled for both spatial proximity and foundress number and, in heterospecific comparisons, habitat.

All statistical tests are two-tailed, and the sample size (N) is the maximum number of matched sets of colonies available for statistical analysis.

RESULTS

Both species of *Polistes* exhibited marked differences in colony productivity in different habitats. *P. fuscatus* displayed significant differences in productivity among the three habitats for mean number of cells ($P = 0.0005$) and mean number of meconial cells ($P = 0.022$; Tables 1, 2). *P. fuscatus* colonies in the forest habitat were significantly less productive than comparable conspecific colonies in the ecotone and old field habitats ($P < 0.01$ for mean number of cells and $P < 0.02$ for mean number of meconial cells). However, colonies of *P. fuscatus* in the ecotone and old field habitats did not differ significantly ($P > 0.05$) in either mean number of cells or mean number of meconial cells (Tables 1, 2).

Polistes dominulus also displayed significant differences in colony productivity among the three habitats for both mean number of cells ($P = 0.003$) and mean number of cells with meconia ($P = 0.015$; Tables 1, 2). Colonies of *P. dominulus* in the old field habitat were significantly more productive ($P < 0.01$ for mean number of cells, $P < 0.02$ for mean number of meconial cells) than comparable conspecific colonies in ecotone and forest habitats (Tables 1, 2). *P. dominulus* colonies in all three habitats differed significantly from each other in mean number of meconial cells ($P < 0.02$) although forest and ecotone colonies did not differ significantly in mean number of cells ($P > 0.05$; Tables 1, 2).

Polistes dominulus was significantly more productive than *P. fuscatus* in all three habitats for both mean number of cells and mean number of meconial cells (Table 3). Depending on the habitat, *P. dominulus* colonies had productivities that were 2.29 to 4.2 times that of comparable colonies of *P. fuscatus* (Table 3). Moreover, there was no evidence that *P. fuscatus* was more competitive with *P. dominulus* in a particular habitat. The productivity ratios of *P. dominulus* vs. *P. fuscatus* did not differ significantly among the three habitats for either mean number of cells ($P = 0.87$) or mean number of meconial cells ($P = 0.17$, Kruskal Wallis tests for both comparisons).

Unexpectedly, *P. dominulus* colonies in the ecotone habitat ($P = 0.024$) and in the old field habitat ($P = 0.00015$) had significantly higher proportions of their cells that contained meconia than comparable colonies of *P. fuscatus*. In the forest habitat, however, the two species had virtually identical proportions of cells with meconia (Table 4). Thus, in the ecotone and old field habitats, *P. fuscatus* colonies had significantly greater percentages of their cells that had not been used to rear brood than comparable colonies of *P. dominulus*.

DISCUSSION

Our results indicate that habitat type had a pronounced effect on colony productivity in both *P. fuscatus* and *P. dominulus*. More specifically, colonies in oak forest habitats were significantly less productive than colonies in ecotone or old field habitats. Colonies of *P. dominulus* were especially productive in old field habitats.

Although our study was not designed to identify the specific environmental factors that contributed to the productivity differences in the three habitats, we believe that the relative amount of sunlight (insolation) was likely a major factor. In general, those habitats with the greatest insolation had the highest colony productivities. Brood stadia in *P. fuscatus* are known to be affected by

Table 1. Colony productivity (mean number of cells/colony ± SD) of the paper wasps *Polistes fuscatus* and *P. dominulus* in three different habitats (forest, ecotone, and old field). The sample size (N) is the number of matched sets of colonies.

	Mean Number of Cells/Colony ± SD				
	(Forest)	**(Ecotone)**	**(Old Field)**	**N**	***P****
P. fuscatus	59 ± 36a	99 ± 57b	108 ± 63b	22	0.0005
P. dominulus	122 ± 79a	156 ± 104a	264 ± 115b	20	0.003

*Friedman tests. Different letters within species denote significant differences in productivity among different habitats (SNK tests, $P < 0.01$).

Table 2. Colony productivity (mean number of meconial cells/colony ± SD) of the paper wasps *Polistes fuscatus* and *P. dominulus* in three different habitats (forest, ecotone, and old field). The sample size (N) is the number of matched sets of colonies.

	Mean Number of Cells/Colony ± SD				
	(Forest)	**(Ecotone)**	**(Old Field)**	**N**	***P****
P. fuscatus	33 ± 23a	58 ± 46b	61 ± 50b	22	0.022
P. dominulus	67 ± 56a	104 ± 94b	203 ± 104c	20	0.015

*Friedman tests. Different letters within species denote significant differences in productivity among different habitats (SNK tests, $P < 0.02$).

Table 3. Comparisons of colony productivity (mean number of cells and meconial cells ± SD) between the paper wasps *Polistes fuscatus* and *P. dominulus* in three different habitats (forest, ecotone, and old field). The sample size (N) is the number of matched sets of *P. fuscatus* and *P. dominulus* colonies.

	Forest (N = 16)			Ecotone (N = 19)			Old Field (N = 24)		
	(*P. fuscatus*)	**(*P. dominulus*)**	***P****	**(*P. fuscatus*)**	**(*P. dominulus*)**	***P****	**(*P. fuscatus*)**	**(*P. dominulus*)**	***P****
Mean No. of Cells	59 ± 34	141 ± 78	0.0005	91 ± 59	220 ± 117	0.001	118 ± 76	287 ± 133	0.0001
Mean No. of Meconial Cells	35 ± 27	80 ± 57	0.003	51 ± 49	159 ± 107	0.001	56 ± 41	235 ± 132	0.0001

*Wilcoxon signed-ranks tests.

Table 4. Proportions of cells (mean ± SD) that contain meconia for colonies of *P. fuscatus* and P. *dominulus* in three different habitats (forest, ecotone, and old field). The sample size (N) is the number of matched sets of colonies.

	P. fuscatus	***P. dominulus***	**N**	***P****
Forest	0.54 ± 0.17	0.54 ± 0.1	16	1.0
Ecotone	0.46 ± 0.24	0.63 ± 0.26	19	0.024
Old Field	0.44 ± 0.18	0.76 ± 0.16	24	0.00015

* Wilcoxon signed-ranks tests.

temperature (West Eberhard 1969, Klahn 1981), which almost certainly affects colony productivity. Klahn (1981) reported that the amount of prey fed to larvae also affects larval stadia and colony productivity. It may be that more open habitats (e.g., old fields) provide *Polistes* colonies higher temperatures and greater availability of insect prey than less open habitats.

We found that *P. dominulus* was significantly more productive than *P. fuscatus* in all three habitats. Furthermore, we found no evidence that *P. fuscatus* was more competitive with *P. dominulus* in any of the three habitats, including the forest habitat. Thus, our data do not provide support for the suggestion that *P. fuscatus* may be more competitive with *P. dominulus* in undisturbed or forest habitats (Gamboa et al. 2004, Liebert et al. 2006).

One could argue that our nestboxes do not approximate natural nesting conditions, including those in a forest habitat. In particular, our plywood nestboxes contain a metal screen that excludes vertebrate predators. Natural nests of *Polistes*, including nests attached to vegetation and in cavities, are vulnerable to vertebrate predators. If *P. dominulus* colonies are more susceptible to vertebrate predation than colonies of *P. fuscatus, P. fuscatus* might enjoy an advantage over *P. dominulus* in those habitats where it nests naturally and is exposed to vertebrate predation. We believe this is unlikely. Silagi et al. (2003), Gamboa et al. (2004), and Liebert et al. (2006) have provided evidence that *P. dominulus* is actually less susceptible to predation by birds and mammals than *P. fuscatus*.

We cannot exclude the possibility that naturally nesting colonies of *P. fuscatus* might have certain advantages over *P. dominulus* in some habitats and persist in those habitats. With the possible exception of enhanced survivorship during winter diapause, however, we are not aware of any behavioral, ecological, or physiological attributes of *P. fuscatus* that would allow it to out-compete *P. dominulus* and to persist in a habitat in which it is sympatric with *P. dominulus*.

Finally, it is not clear why *P. fuscatus* had such a large proportion of its cells unused in ecotone and old field habitats when compared to *P. dominulus*. It may be that queens of *P. fuscatus* were unable to lay eggs in many cells because of their poorer physical condition. Queens of *P. dominulus* have been reported to have a higher survivorship than queens of *P. fuscatus* (Gamboa et al. 2002). This enhanced survivorship of *P. dominulus* queens has been attributed to their lack of conspecific usurpation pressures and the tendency of *P. dominulus*, unlike *P. fuscatus*, to maintain extensive stores of nectar in the comb (Silagi et al. 2003). Nevertheless, the question of why combs of *P. fuscatus* had such large proportions of their cells unused merits further study.

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