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HIGH PRODUCTIVITY IN HAPLOMETROTIC COLONIES OF THE INTRODUCED PAPER WASP *POLISTES DOMINULUS* (HYMENOPTERA: VESPIDAE; POLISTINAE)

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Abstract.—The intrinsic rate of increase of a population in terms of fecundity, developmental time, and longevity, is known to affect the colonizing ability of species. We present evidence that *Polistes dominulus,* an invasive European paper wasp introduced to the United States, exhibits life-history traits that predispose it to successful colonization. This predisposition is not simply due to the more frequent pleometrosis of *P. dominulus.* Many authors have speculated, based on cursory observations, that *P. dominulus* is replacing native species including *P. metricus.* The possibility of replacement in light of the data is discussed.

Key words: Competitive exclusion, productivity, *Polistes dominulus*.

INTRODUCTION

Polistes dominulus was first reported in Cambridge, Massachusetts in 1981 (Hathaway, 1981, cited as *Polistes gallicus*). It has a contiguous range west to Wisconsin and at least as far south as Virginia, but has also been discovered in California (AMNH specimen, OSU Hymenoptera Online Database ID = OSUC 80429). Once it invades a new area, its presence becomes noticed increasingly in cities and some have commented on the possibility that *P. dominulus* is competing with native species to their exclusion (Hathaway, 1986; Judd and Carpenter, 1996; Wegner, 1997). These comments have ranged from dismissal of the idea of competitive exclusion (Hathaway, 1986), to the cautious urging of further study (Judd and Carpenter, 1996), to complete endorsement (Wegner, 1997). Hathaway (1986) noted that *P. dominulus* does not appear to compete with native *Polistes* for nest sites, and also stated ‘‘their foraging strategies are different.’’ Judd and Carpenter (1996) speculated conservatively about the possible exclusion of native wasps by *P. dominulus,* urging more study: ‘‘*P. dominulus* may have displaced the native *P. fuscatus* to some extent, or may simply be a more accomplished synanthrope.’’ Wegner (1997) states definitively, ‘‘This wasp outcompetes the native species of *Polistes* in urbanized areas, wherever it expands its range.’’

P. dominulus appears to be more common than *P. nimphus* and *P. gallicus* where they are sympatric (Cervo et al., 2000), displaying a 7-fold increase in the number of colonies in artificial shelters after a single season.

The wide variety of viewpoints on this topic is not surprising as competitive exclusion is difficult to investigate. At least three criteria must be demonstrated before competitive exclusion can be proposed: (1) competition for food, space, or some other limiting resource, (2) decreased productivity of both species when the two are sympatric (with one being more severely impacted than the other), and (3) competitive release of both species when they are allopatric (Gause, 1934; Ricklefs, 1990).

Lewontin (1965) discussed the relative importance of three life history traits that effect intrinsic rate of population increase (*r*): fecundity, developmental time, and longevity. His premises were that (1) any increase in fecundity, decrease in developmental time, or increase in longevity (i.e., reproductive lifespan) will enhance the colonizing ability of a population; (2) combinations of these traits will further increase *r* within the population; and (3) that phylogenetic inertia may prohibit the optimal increase of all three life-history traits. His calculations were adapted from the equations of Volterra (1931), which assume an exponentially increasing population. These predictions are generally easily tested by the simple comparison of life-table parameters [e.g., $V(x) = l(x)m(x)$] (Lotka, 1956; MacArthur and Wilson, 1965), however, the assumption of exponentially increasing population size does not hold for populations with a significant reproductive skew such as social insects (Oster and Wilson, 1978).

Oster and Wilson (1978) proposed productivity models suited for social insects. Ultimately, their model suggests that a social insect's colony can be viewed (in terms of productivity) as the investment in worker production and the investment in the production of reproductives. As the worker population increases, it reinvests a portion of its gathered resources toward the production of either more workers or reproductives. As a consequence, this so-called ''return-function'' determines the production of new colony members. Ultimately, fitness is a measure of the number of reproductives produced at the end of the colony cycle who (1) succeed in mating, (2) survive the winter, (3) and successfully found a spring colony. Along these lines, we directed our investigations toward the particular colony attributes that reveal the overall fitness of the colony. These attributes include: nest construction (i.e., the number of cells in a nest), developmental period, worker production, and gyne (future queen) production.

We present data that derive from the investigation of each of these criteria. In our experiments, *ad libitum* food availability in the laboratory was compared with natural foraging in the field. We document productivity of *P. dominulus* and *P. metricus* (the most abundant native species in central Ohio) under laboratory conditions of allopatry and natural sympatry in the field. We contrast the relative productivity of both species in the laboratory (under allopatry) and in the field (under sympatry).

METHODS

Laboratory Colonies. Eighteen gynes of *P. dominulus* and 21 gynes of *P. metricus* were collected in May 1997 from Columbus, Ohio and nearby localities. Most gynes initiated nests in May. We placed each gyne in a separate plastic container (27 cm $\times$ 16.5 cm $\times$ 19 cm) to the roof of which we had previously glued a wooden popsicle stick. If the gyne was collected with her nest, the nest was glued to the wooden stick. All of the colonies were housed in the OSU greenhouse under natural light and outside ambient temperature. Each gyne was supplied with water, rock sugar, and filter paper for nest construction. If the nestless gynes began construction on a surface of the chamber other than the wooden stick, we moved the nest to the stick after she had built two or three cells (usually one day). After brood were present, we supplied the wasps with *Galleria melonella* caterpillars *ad libitum* each day of the experiment. Cell number and worker emergence were recorded throughout the colony period. During the summer, many pupae were removed from the *P. dominulus* colonies as a part of another experiment. This is important as the removed workers are not included in this study's count of emerged workers, permitting only a conservative estimate of productivity. In addition, these workers were obviously unable to contribute to colony development; accordingly, the data for worker emergence and cell number for *P. dominulus* colonies are necessarily reduced. Because all colonies were isolated, these data represent the colony development of the respective species under allopatry.

Field Colonies. Fifteen colonies of *P. dominulus* and nine colonies of *P. metricus* were observed from June through September 1998 at one location in Dublin, OH, USA. The colonies of both species were constructed on four abandoned barns in an old field near a heavily wooded area. The colonies were observed every other day, and data on cell construction, pupal initiation, and worker emergence were recorded from June 16 to August 30. The queen disappeared from three *P. dominulus* colonies and one *P. metricus* colony during the study. If it were known that the missing wasps had died or renested, they could be counted toward a measure of productivity, but as their fate and ultimate contribution could not be determined, their known progeny had to be eliminated from estimates presented here.

Both *P. dominulus* and *P. metricus* produce haplometrotic and pleometrotic colonies. Pleometrosis is known to correlate with increased productivity in both species (Grechka and Kipyatkov, 1984; Gamboa, 1978, 1980), and *P. dominulus* is more frequently pleometrotic than *P. metricus.* As such, we wished to determine if factors other than frequency of pleometrosis explain productivity differences. Therefore we focused exclusively on singly-founded nests. Three of our *P. dominulus* field nests were founded by multiple females, and these colonies were excluded from the final analysis so that the productivity of single queen colonies could be compared across the species. The excluded nests, added, of course, to real-life productivity in the field outside of estimates presented here.

Because of these reasons, the aims of which were to produce comparable estimates of productivity while holding many variables constant, the data from eight *P. dominulus* nests and eight *P. metricus* nests were analyzed.

RESULTS

Cell Number. Figure 1 shows the number of cells per colony for both species at the end of the colony cycle in isolated, laboratory colonies. The difference in distributions is highly significant (Fig. 1: Mann-Whitney *U*-test, $P \ll 0.001$). The development of the field colonies in terms of cell number varied greatly within and between species. Figures 2A and B show cell production for each colony of *P. dominulus* and *P. metricus,* respectively, over the course of the colony cycle in the field. The smallest field colony of *P. dominulus* reached a size of 35 cells, while the smallest *P. metricus* field colony had 13 cells (Fig. 3A). The largest colony of *P. dominulus* obtained a cell number of 415 cells, and the largest *P. metricus* nest reached a size of 84 cells (Fig. 3B). The date of first worker emergence was used as a standard for comparison. At the time of first worker emergence, *P. dominulus* colonies were composed of significantly more cells (Table 1: Mann-Whitney *U*-test, $P < 0.001$). At one month after the emergence of the first worker, the disparity had more than doubled (Table 1: Mann-Whitney *U*-test, $P < 0.005$). By the end of the

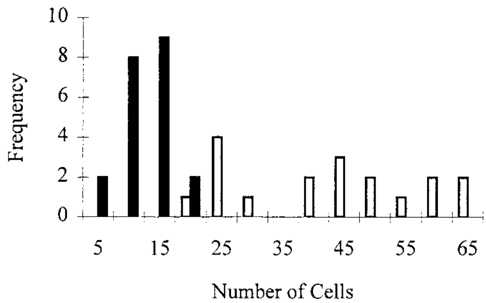

Fig. 1. Number of Cells at End of Colony Cycle in Lab. The difference in median values is significant at $P \ll 0.001$ (Mann-Whitney *U*-test). *P. dominulus* (white bars); *P. metricus* (black bars).

colony cycle in the field, the disparity had doubled again (Table 1: Mann-Whitney *U*-test, $P < 0.001$), with *P. dominulus* colonies producing nearly 7 times the cells per nest as *P. metricus.*

Number of individuals produced and developmental period. Figure 4 shows the number of individuals present at the end of the colony cycle in isolated, laboratory colonies. The difference in distributions between *P. dominulus* and *P. metricus* colonies is highly significant (Mann-Whitney *U*-test, $P \ll 0.001$).

In laboratory colonies, the median date of first worker emergence was significantly earlier for *P. dominulus* colonies (Table 2: Mann-Whitney *U*-test, $P \ll 0.001$). In field comparisons, *P. dominulus* colonies produced the first wave of workers two days prior to *P. metricus* colonies. Eliminating *P. metricus* colonies that never reproduced suggests that the dates of first worker emergences were not significantly different (see Table 2) using a standard non-parametric statistic. However, a fair calculation of productivity would include failed nests (Michener, 1964). Therefore we assigned failed nests a value beyond the end of the colony cycle (day = 215), indicating that up until the last day of the season, no offspring were produced. When these colonies are included (*P. metricus,* N = 3 colonies), *P. dominulus* workers did emerge significantly earlier than *P. metricus* workers (''Adjusted median in field'' of Table 2: Mann-Whitney *U*-test, $P < 0.05$).

Figure 5 shows that *P. dominulus* achieves significantly more of its total productivity early (Fig. 5: Kolmogorov-Smirnov, D_1 = Day 160 $P < 0.01$, D_2 = Day 181, $P < 0.001$). *P. dominulus* colonies produced half of their total offspring by day 158, whereas *P. metricus* did not until day 183.

Gynes. Workers are not easily separated from gynes in *Polistes* as there are not obvious morphological differences between castes (West-Eberhard, 1969; Wilson, 1971; but see O'Donell, 1998). In our field study, we considered all individuals that left the nest near the end of the colony cycle gynes. Table 3 shows that *P. dominulus* colonies produce more individuals (N = 106) and gynes (N = 45) than *P. metricus* colonies (individuals: N = 21; gynes: N = 4). More dramatically, *P. dominulus* gynes outnumber all individuals produced by *P. metricus* colonies (N = 21). Even when one large *P. dominulus* colony (colony 9; N gynes = 25) is removed from the analysis, the remaining *P. dominulus* gynes (N = 20) number only one less than all

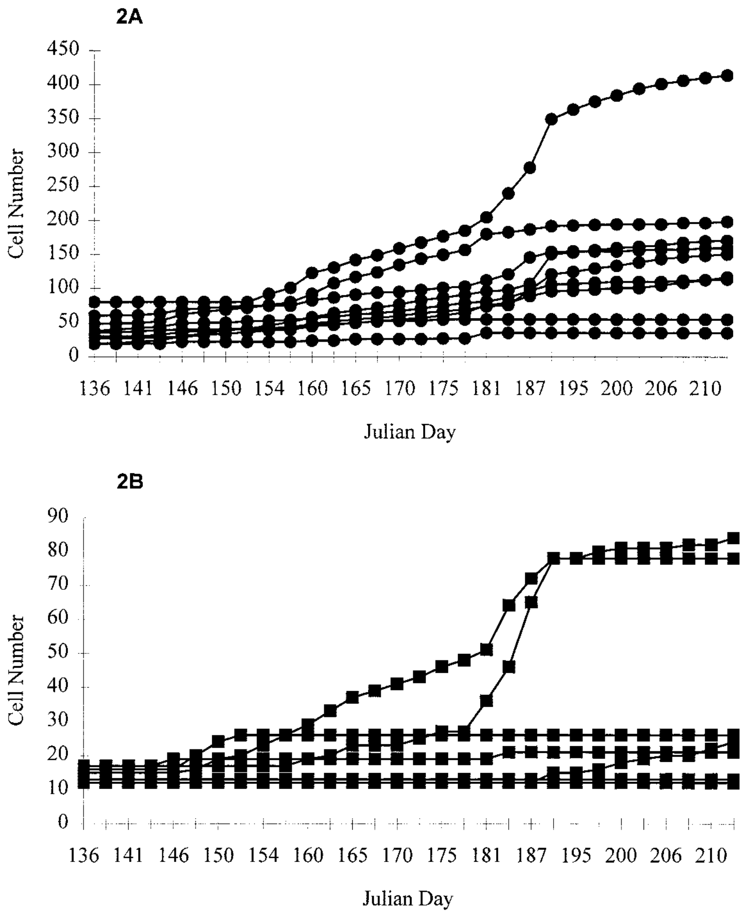

Fig. 2A, B. Cell construction patterns over the course of the colony cycles in the field for all *P. dominulus* (2A) and *P. metricus* (2B) colonies observed. Note difference in scales.

individuals, including non-reproductives, produced on *P. metricus* nests (N = 21). The *P. metricus* colonies produced 2 males total.

DISCUSSION

We have shown that *P. dominulus* colonies produce more cells than *P. metricus* colonies throughout the colony cycle (see Table 1). The fact that this occurred in both laboratory and field colonies, coupled with data from previous studies of these species demonstrating the same phenomenon (Rabb, 1960 for *P. metricus*; Turillazzi, 1980 for *P. dominulus* in Europe) suggests that this is not due to competitive factors. We have presented evidence that *P. dominulus,* under conditions of both laboratory-induced allopatry and natural sympatry, is naturally more productive than *P. metri-*

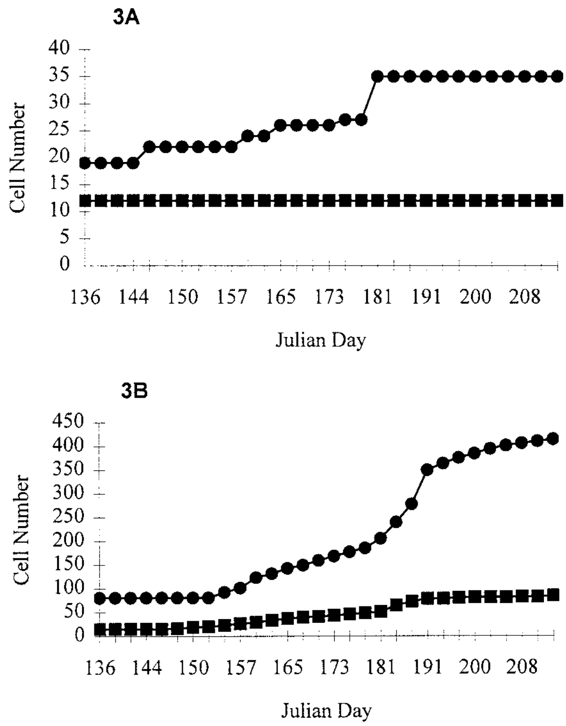

Fig. 3A, B. The smallest field colonies in terms of cell number for both species (3A). The largest field colonies in terms of cell number for both species (3B). *P. dominulus* (circle); *P. metricus* (square).

cus, that *P. dominulus* colonies produced adults earlier than *P. metricus* (see Table 2), and that *P. dominulus* colonies are more fecund, in terms of total individuals produced and production of reproductives (see Table 3).

P. dominulus colonies produce first workers significantly earlier in laboratory colonies (Table 3: Mann-Whitney *U* test: $P \ll 0.001$) and marginally significantly earlier in field colonies (Table 3: Mann-Whitney *U* test: $P = 0.067$). Producing individuals earlier in the year can result in greater defense against predators and increased productivity (Gamboa, 1978, 1980). In fact, *P. dominulus* colonies did skew the production of their workers and gynes earlier in the colony cycle (Fig. 5: Kolmogorov-Smirnov: D_1 = Day 160 $P < 0.01$, D_2 = Day 181, $P < 0.001$) . Gamboa (1979, 1980) showed that *P. metricus* individuals require approximately 50 days (taken from all nests for which date of nest initiation and first worker emergence was given) for development, whereas Pardi (1951, cited in Strassmann and Orgren, 1983) showed that *P. dominulus* (cited as *P. gallicus*) in Europe requires an average of 40 days, with the developmental range reaching even below 40. Rabb (1960) found that *P. exclamans, P. fuscatus,* and *P. dorsalis* (cited as *P. hunteri*) required 48 days for development from egg to adult. Our data suggest that *P. dominulus* individuals de-

Table 1. Number of cells over the course of colony development in the field, ranked by final productivity. Values for number of cells constructed at time of first worker emergence, one month after first worker emergence, and total number of cells at end of colony cycle are shown. Median values and *P*-values (Mann-Whitney *U*-test) are shown at the bottom of each category. Three *P. metricus* colonies never produced workers, and therefore values at first worker emergence and one month after first worker emergence are unknowable. Final values are indicated in parentheses.

Productivity rank	Number of cells at time of first worker emergence			Number of cells one month after first worker emergence			Total cells at end of season		
	P. dominulus	*P. metricus*		*P. dominulus*	*P. metricus*		*P. dominulus*	*P. metricus*	
1	80	15		177	46		415	84	
2	49	19		135	78		199	78	
3	39	20		96	26		171	26	
4	69	15		101	22		160	24	
5	40	(21)†		69	(21)†		151	21	
6	29	(13)†		61	(13)†		117	13	
7	50	(12)†		81	(12)†		114	12	
8	36	10		55	10		55	10	
Median	44.50	15.00	$P \ll 0.001$	88.50	26.00	$P < 0.005$	155.0	22.50	$P < 0.001$

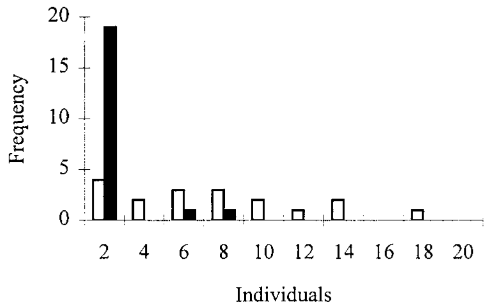

Fig. 4. Number of Individuals at End of Colony Cycle in Lab. The difference in median values is significant at $P \ll 0.001$ (Mann-Whitney U-test). *P. dominulus* (white bars); *P. metricus* (black bars).

velop at least 2 days more quickly than native *Polistes,* and these slight differences can greatly increase the number of *P. dominulus* reproductives over time (Oster and Wilson, 1978).

Judd and Carpenter (1996) suggest that *P. dominulus* may be better at living with humans than native *Polistes.* Although Cervo et al. (2000) proposed that reusing nests in artificial sites might account for some of the high productivity, we show that high productivity occurs even in the absence of nest reuse. We propose an adaptive hypothesis that takes into account *P. dominulus'* synanthropic nature. Paper wasps are known to reinforce their nest material with various oral secretions (West-Eberhard, 1969; Jeanne, 1972; Downing and Jeanne, 1983, 1987; Wenzel, 1991; Singer et al., 1992; Downing, 1994; Kudô, 1998). These secretions are largely proteinacious and reproductively costly; between 14.2% and 19.6% of nitrogenous material harvested by foragers is added to the nest, and this is therefore not used to nourish the brood (Kudô, 1998). In the USA *P. dominulus* nests are easily distinguished from native *P. metricus* and *P. fuscatus* nests by their more papery and fragile appearance. The paper material of *P. dominulus* nests is of a grayer color, whereas native nests are darker and seem to have more secreted material embedded in their fibers. This apparent discrepancy in nest reinforcement makes adaptive sense

Table 2. Dates of first worker emergence for laboratory and field colonies. Median dates are given for laboratory and field colonies. The difference in median date of first worker emergence in the laboratory is highly significant (Mann-Whitney U-test, $P \ll 0.001$). The median dates of first worker emergence in the field show no significant difference. Three colonies of *P. metricus* failed ever to produce workers. If those three colonies are considered to have taken 215 days to produce offspring (the entire growth season), then the difference in median date of first worker emergence (indicated as "Adjusted") is significantly earlier for *P. dominulus* field colonies (Mann-Whitney U-test: $P < 0.05$).

	P. dominulus	*P. metricus*	*P*-value
In laboratory	June 25	July 26	$\ll$0.001
In field	June 26	June 28	N.S.
Adjusted median in field	June 26	July 27	$<$0.05

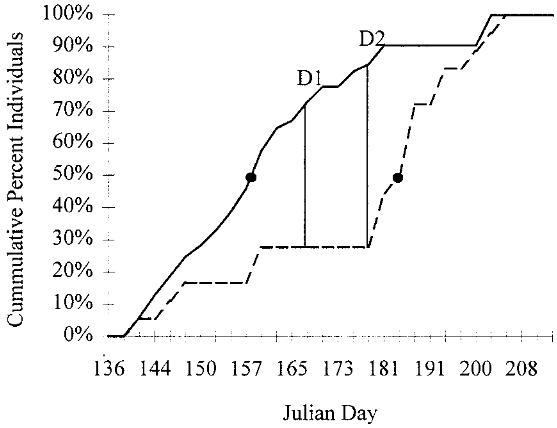

Fig. 5. Cumulative percent of individuals of all colonies for each species. *P. dominulus* (solid line) achieves significantly more of its total productivity early (Fig. 5: Kolmogorov-Smirnov, D_1 = Day 160, $P < 0.01$, D_2 = Day 181, $P < 0.001$). *P. dominulus* colonies produced half of their total offspring by day 158, whereas *P. metricus* did not until day 183 (black ovals).

when it is considered that the amount of oral secretion added to paper wasp nest material is positively correlated with exposure to rainfall (Yamane and Itô, 1994; Kudô, 1998). As *P. dominulus* has co-existed with a ubiquitous human civilization in Europe for centuries longer than have North American *Polistes,* the opportunities to build nests under protected human constructions have been historically high for *P. dominulus* and low for *P. metricus* and *P. fuscatus.* Apparently, the *P. dominulus* individuals that founded the North American population invest less to waterproof their nests, thus allowing for an increased percentage of proteinacious material being shunted to the brood. If this is confirmed, it could explain *P. dominulus'* increased fecundity.

Alien species may enjoy high reproductivity in their new environments if local parasites are not adapted to the aliens, and there is reason to believe that this happens

Table 3. Individuals and gynes produced in field colonies. *P. dominulus* colonies produced more individuals than did *P. metricus* colonies (Mann-Whitney *U*-test, $P < 0.01$). *P. dominulus* colonies also produced more individuals who left the nest in August (treated here as gynes) than did *P. metricus* colonies, though when the median is taken, the values are marginally significant (Mann-Whitney *U*-test, $P = 0.067$) because a few nests produced most of the gynes.

	P. dominulus	*P. metricus*	*P*-value
Max. No. individual across all colonies	106	21	
(N = colonies)	(N = 8)	(N = 8)	
Median (expected) # individuals	6.00 (13.3)	0.00 (2.6)	<0.01
No. individuals leaving nest	45	4	
(N = colonies)	(N = 8)	(N = 8)	
Median (expected) # gynes	3.00 (5.6)	0.00 (.5)	= 0.067

with *P. dominulus.* The Strepsiptera is a bizarre order of parasitic insects that subsist on the hemolymph of many insects, including *Polistes* spp. In the United States, Strepsiptera in the genus *Xenos* can negatively impact *Polistes* by retarding larval development (Wheeler, 1910), disrupting the oviposition apparatus (K. Pickett, pers. obs.), shortening adult life and decreasing the likelihood that a reproductive will survive the winter (Salt, 1927). In Europe, *P. dominulus* can become infected with *X. vesparum.* However, *X. vesparum* has never been discovered in North America. We collected *Polistes fuscatus*, the most common native wasp in New York, and *P. dominulus* from Ithaca, NY just prior to the peak *Xenos* emergence period (early September) during 1997 and 1998. Of 68 *P. fuscatus* individuals collected in 1997, and 44 collected in 1998, 16.2% and 18.2% were infected, respectively. However, of 1,123 *P. dominulus* individuals collected over the two year period, none where strepsipterized (These values, based on extensive surveys over two years are to be preferred over the 7% to 10% rates reported in Cervo et al. [2000] and attributed to us). These data suggest that *P. dominulus* does not become infected with North American *Xenos* spp. and therefore does not incur the negative impacts of being strepsipterized that native *Polistes* incur.

IS *POLISTES DOMINULUS* COMPETITIVELY EXCLUDING NATIVE PAPER WASPS?

Polistes dominulus' high intrinsic rate of reproductive increase is not, in itself, sufficient to warrant the conclusion that this invasive species will outcompete native populations to their extinction. Certainly, the seemingly apparent ''replacement'' phenomenon that has been discussed casually in the literature (Hathaway, 1986; Judd and Carpenter, 1996; Wegner, 1997) is due to personal observations of the apparently increasing *P. dominulus* population density. But this alone will not result in competitive exclusion. A crowded population, resulting in a shortage of food, is usually required for competition to ensue, but this requires the populations to approach or exceed the carrying capacity.

Competitive exclusion need not be invoked to explain the abundance of *P. dominulus* in North America. *Polistes dominulus* has a plastic food repertoire (KMP and JWW, pers obs.). Perhaps *P. dominulus* is not in direct food competition with native *Polistes*, which tend to have strict diets, specializing on caterpillars (Rabb 1960). Specialists can co-exist easily when relying on different mixtures of prey, even if they eat the same prey (MacArthur and Levins, 1964). Many species of *Polistes* are sympatric in North America, and these are known to have subtle hunting and diet differences which may explain why the more productive *P. annularis* does not exclude other *Polistes* from its range (Hermann and Dirks, 1975; Rabb, 1960). Our data suggest that the same may happen with *P. dominulus.*

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