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Genetics, behavior and ecology of a paper wasp invasion: *Polistes dominulus* in North America

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Studies of social insect invasions to date have focused primarily on highly eusocial insects such as ants and yellowjacket wasps. Yet insect societies without fixed, morphological caste systems may be particularly good invaders due to their behavioral flexibility, as demonstrated by the recent invasion of the European paper wasp *Polistes dominulus* into North America. Here we provide a review of this ongoing invasion in terms of (1) population genetic variation in *P. dominulus*, and (2) comparative behavior and ecology of *P. dominulus vs*. the native *P. fuscatus*. We present new genetic evidence supporting the occurrence of multiple independent introductions of *P. dominulus* into the USA, confirming previous results demonstrating relatively high genetic variation in introduced populations. We also present behavioral and demographic evidence suggesting that *P. dominulus* is displacing the native *P. fuscatus* in at least part of its range, most likely due to the superior productivity and survivorship of *P. dominulus* colonies. We review data from comparative studies where the two species are sympatric and discuss possible mechanisms contributing to the differences between them. Finally, we discuss the ecological impacts of this invasion and the role of *P. dominulus* as a model organism for invasion biology.

Introduction

The accidental introduction of the paper wasp *Polistes dominulus* (Christ) into North America has provided an excellent opportunity to examine the pattern and process of invasion biology via genetic, behavioral and ecological studies. In our review, we address major questions about this invasion: Is the spread across North America from one introduction? Is there any evidence of genetic bottlenecks as might be expected when small numbers of individuals are introduced? Is *P. dominulus* displacing native *Polistes*? If so, then by what mechanisms is displacement occurring? We attempt to answer these questions by reviewing existing literature and introducing new data that address genetic, behavioral and ecological aspects of this invasion. First, we compare the genetic variation of several introduced populations of *P. dominulus* with that of a population in its native range. Second, we address the question of whether *P. dominulus* is displacing native *Polistes* in North America. Third, we provide a comprehensive behavioral and ecological comparison of *P. dominulus* and one North American native species, *P. fuscatus* (F.), including discussion of specific mechanisms that may be contributing to the widespread success of *P. dominulus* in its introduced range. This review, therefore, represents a thorough and comprehensive examination of this ongoing invasion.

The value of studying invasions

Biological invasions are so pervasive that they have been recognized as an important component of global environmental change (Vitousek *et al.* 1996). Because of the irreversibility of mixing formerly isolated species, biological invasions may have even more drastic effects than climate change (Mooney & Cleland 2001). With the rate of such invasions likely to continue increasing with free trade and global commerce (Levine & D'Antonio 2003), it is important to understand the processes that promote and accompany the spread of introduced species. Such studies contribute basic knowledge about evolutionary and ecological processes, and may impact conservation and management decisions (Holway & Suarez 1999, Sakai *et al.* 2001, Hänfling & Kollmann 2002, Lee 2002, Allendorf & Lundquist 2003).

Invasions can serve as "natural experiments", providing opportunities for ecological and evolutionary insight (Chapman & Bourke 2001, Mooney & Cleland 2001, Sakai *et al.* 2001, Giraud *et al.* 2002, Hänfling & Kollmann 2002, Lee 2002, Lambrinos 2004). Most early studies focused only on the ecological impacts of invasions, primarily in terms of the immediate effects of invading species on native communities and ecosystems (Lambrinos 2004). More recently, the role of genetic diversity in influencing invasion success has become an important area of research (Lee 2002, Parker *et al.* 2003). In small populations, such as those on islands, reduced genetic diversity due to genetic drift and inbreeding is implicated in higher extinction rates (Frankham 1998, Frankham & Ralls 1998). Similarly, populations of introduced species that undergo a genetic bottleneck during colonization may have a reduced chance of success.

Allendorf and Lundquist (2003) point out two paradoxes regarding the success of invaders despite apparent impediments to their establishment in novel environments:

1. If genetic variation is necessary for successful adaptation to new environments, how do introduced species become successful invaders if genetic variation is lost upon founding a new population?
2. If species are introduced to novel habitats, how can they successfully out-compete or even replace locally adapted native populations that have evolved in that environment?

Recent studies have begun to address the first paradox mentioned above by measuring genetic diversity and identifying genetic bottlenecks in introduced populations (e.g., Fonseca *et al.* 2000, Tsutsui *et al.* 2000, Zeisset & Beebee 2003, Rasner *et al.* 2004). Interestingly, although bottlenecks have been found to decrease population success in some cases (e.g., increased hatching failure in birds, Briskie & Mackintosh [2004]), other studies have found no adverse effects of genetic bottlenecks, perhaps due to rapid population expansion after colonization (e.g., Cabe 1998, Le Page *et al.* 2000, Zeisset & Beebee 2003). With a high population growth rate, relatively high levels of heterozygosity can be maintained even if there has been a genetic bottleneck, especially if the bottleneck was not severe or if there were multiple colonizing individuals (Nei *et al.* 1975).

Enhanced invasion success after a genetic bottleneck is also possible. A striking example is the invasion of North America by Argentine ants (*Linepithema humile*), which coexist with many ant species in their native regions of South America but exclude heterospecifics in California (Suarez *et al.* 1999). The success of this invasion has been attributed to reduced intraspecific aggression and subsequent "supercolony" formation in introduced populations (Suarez *et al.* 1999). It is thought that this unusual social structure arose because of a genetic bottleneck upon introduction, which reduced the variation of recognition alleles and prevented individuals from discriminating nestmates from non-nestmates based on genetic similarity (Tsutsui *et al.* 2000, 2003, Tsutsui & Case 2001). Thus, the paradox may be resolved via rapid population growth after a brief bottleneck, or via positive, indirect effects of reduced genetic diversity on previously adaptive behavior such as nestmate recognition (*see* Starks 2003).

Alternatively, the paradox may be irrelevant for some introduced populations in which no loss of genetic diversity occurs. In fact, genetic diversity may even be increased relative to native populations if there are multiple introductions from sources within a substructured native range (Sakai *et al.* 2001, Lee 2002, Parker *et al.* 2003, Kolbe *et al.* 2004). A clear example of this was shown in a study of invasive brown anole lizards in Florida, where the distribution of mtDNA haplotypes suggested at least eight introductions from across the native range of this species (Kolbe *et al.* 2004). In this situation, novel genotypes can arise from combinations of alleles not found together in the native range.

The second paradox, how introduced species successfully compete with locally adapted native species, can be resolved in several ways. First, the lack of local adaptation may be a benefit to introduced species, for example, if they face less pressure from natural enemies that have coevolved with native species. Some invaders may also evolve local adaptations relatively quickly after colonization. Indeed, this process may explain the "lag phase" of many introduced populations, where growth remains slow until sudden rapid expansion (Sakai *et al.* 2001, Lee 2002). Local adaptation also requires sufficient genetic variation in the introduced population for selection to act upon, and could result in a general decrease in population genetic diversity. Alternatively, invaders may succeed because of phenotypic plasticity. Many "weedy" species are known to have generalist habits and to be tolerant of a broad range of conditions (Baker 1965, Sakai *et al.* 2001, Lee 2002, Parker *et al.* 2003). These characteristics may also work in concert, with phenotypic plasticity being crucial in the early stages and local adaptation becoming more important at a later stage (Sexton *et al.* 2002, Lambrinos 2004).

Social insect invasions

Social insects are known to be effective invaders (reviewed in Moller [1996], Chapman & Bourke [2001]). Many social insects fit the description of "weedy" species; they tend to be adaptable to a variety of environments, including human-disturbed habitats, and they often have a generalist diet, feeding their larvae various arthropod fauna. Sociality itself may also allow these insects to be more flexible in adapting to new environments because the loss of one individual from a colony is less detrimental than loss of an individual of a solitary species (Moller 1996).

Until now, studies of insect invasions have focused almost exclusively on either solitary-living agricultural pests or the highly eusocial ants and yellowjacket wasps. *Polistes* wasps are also eusocial, meaning they have overlapping generations, cooperative brood care, and a reproductive division of labor (Wilson 1971). However, the eusociality of ants and yellowjacket wasps is characterized by fixed, morphologically distinct reproductive castes ("advanced" eusociality). In contrast, *Polistes* wasps have a more flexible caste system ("primitive" eusociality); although all *Polistes* females can reproduce, some assume subordinate roles to help others raise offspring. *Polistes* species occasionally have even been found to demonstrate subsociality, in which offspring disperse and there is no "worker" caste (*P. aurifer*, Liebert *et al.* [2005a]; *P. biglumis*, Lorenzi & Turillazzi [1986]; *P. fuscatus*, Reeve *et al.* [1998]; *P. dominulus*, Starks [2001]). With respect to sociality and behavioral plasticity, the system of "primitive" eusociality represents a considerably understudied group within the field of invasion biology.

We begin here to address this gap with a comprehensive review of the *P. dominulus* invasion in the United States. We describe the current state of this invasion in terms of (1) population genetic variation, and (2) comparative behavior and ecology of *P. dominulus vs*. the native *P. fuscatus*. We also discuss the potential ecological impacts of this invasion and the role of *P. dominulus* as a model organism for the study of invasion biology.

The *P. dominulus* invasion: timeline and biogeography

Although *P. dominulus* is most common in Mediterranean Europe and North Africa, its native range spreads across eastern Europe and as far as China (Cervo *et al*. 2000). Since the mid-1980s, this range has expanded to include the relatively cooler climates of northern and eastern Europe (Pekkarinen & Gustaffson 1999). This expansion may reflect temperature increases in these newly invaded areas with the global warming of the last 100 years (IPCC 1996, 2001), and/or an expansion of modern urban-suburban environments that provide warmer habitats than rural and less disturbed areas (von Stulpnagel *et al*. 1990). In addition to its presence in Europe, Asia, and Africa, *P. dominulus* has also been accidentally introduced to western Australia (Cardale 1985), South America (Chile; Willink & Chiappa 1993), and North America (Eickwort 1978, Hathaway 1981). Populations have subsequently become established in all of these locations; thus *P. dominulus* has successfully colonized every continent where social insects are found.

The first North American occurrence of *P. dominulus* was reported in Massachusetts in the late 1970s (Eickwort 1978), and by 1995 this species had been documented throughout the northeastern USA (reviewed in Judd & Carpenter [1996]). In the decade since (1996–2005), *P.*

Table 1. Summary of *P. dominulus* reports in the United States and border regions of Canada. The four sites represented in the current study are indicated with boldface.

Year	Lat. °N/Long. °W	State/Province	Reference
1978	**42.38**, **71.12**	**Massachusetts, USA**	Eickwort 1978, Hathaway 1981
1986	40.66, 74.31	New Jersey, USA	Jacobson 1986, 1988
1991	42.45, 76.47	New York, USA	Jacobson 1991a
1991	41.51, 81.56	Ohio, USA	Jacobson 1991b, 1994
1991	40.01, 75.13	Pennsylvania, USA	Jacobson 1991a
1991	44.01, 73.12	Vermont, USA	probable sighting; Jacobson 1991b
1992	41.31, 72.92	Connecticut, USA	Menke 1993
1995	39.00, 76.93	Maryland, USA	Staines & Smith 1995, Jacobson 1996
1995	**42.69**, **83.12**	**Michigan, USA**	Judd & Carpenter 1996
1995	43.47, 70.44	Maine, USA	Russo 1996
1996	38.64, 90.24	Missouri, USA	Arduser & Stevens 1999
1997	43.09, 79.02	Ontario, Canada	Hoebeke & Wheeler 2005
1998	**38.57**, **121.47**	**Northern California, USA**	pers. comm. by Carpenter, cited in Cervo *et al.* 2000
1998	46.32, 120.01	Washington, USA	Landolt & Antonelli 1999
1999	40.78, 111.03	Utah, USA	http://extension.usu.edu/files/factsheets/EuropeanWasp.pdf
2001	**34.06**, **118.44**	**Southern California, USA**	P. Nonacs pers. comm.
< 2002	41.87, 88.15	Illinois, USA	http://www.cirrusimage.com/Bees_wasp_polistes.htm
2003	40.56, 105.07	Colorado, USA	http://www.coopext.colostate.edu/TRA/PLANTS/index.html
2003	43.61, 116.23	Idaho, USA	http://www.idl.idaho.gov/invasivespecies/invasive_species_resources/idaho_assessment.pdf
2003	45.32, 118.09	Oregon, USA	La Grande specimen ID, 2003; J. Carpenter, pers. comm.
2003	48.58, 123.40	British Columbia, Canada	Borkent & Cannings 2004
< 2003	38, 77	Virginia, USA	http://butterflywebsite.com/articles/monarchwatch/newsletter.cfm?n=dec2003.txt
2004?	43, 89	Wisconsin, USA	http://insects.entomology.wisc.edu/Hymenoptera/vespoidea/vespidae/
2004?	44.95, 93.10	Minnesota, USA	http://www.extension.umn.edu/yardandgarden/YGLNews/YGLN-July0104.html#wasp

dominulus was also observed in Canadian provinces and many western USA states ranging from Missouri to California (Table 1). It is likely that the species is also present in additional states but has not yet been reported.

Although *P. dominulus* colonization has generally moved from east to west across the USA (Table 1), little is known about its mechanism of dispersal. Repeated introductions may be especially likely in this genus because gynes frequently overwinter in narrow spaces within human-made structures and may be hidden inside transportable items such as shipping crates, trailers, boats, etc. Because females store sperm, a single individual can initiate a colony and produce many reproductives (Moller 1996, Chapman & Bourke 2001). Moreover, because of frequent North American trade with countries throughout the native range of *P. dominulus*, and the ability of *P. dominulus* to be moved around the country by vehicular transport (e.g., Landolt & Antonelli 1999), it is likely that the current range of *P. dominulus* in North America is due to multiple introductions from sources in its native range as well as expansion of established introduced populations.

Genetics of the *P. dominulus* invasion

Despite mounting interest in understanding how genetic diversity influences the success or failure of newly established populations, surprisingly little work has been done on the population genetics of the *P. dominulus* invasion. In a preliminary investigation of this topic, Johnson and Starks (2004) compared microsatellite genotypes of introduced *P. dominulus* populations with those of a previously studied European sample for which heterozygosity data were available (Henshaw 2000). A total of 79 wasps, each representing a separate colony, were collected in 2001 from four geographically distinct locations within two regions of the northeastern USA: Massachusetts and New York (~444 km apart). Within these regions, two sites were in Massachusetts (23 km apart) and two were in New York (24 km apart). The results showed an unexpected level of genetic diversity in the introduced populations. The northeastern USA population showed no significant reduction in genetic diversity relative to the European sample, and no trace of a genetic bottleneck. Both the Massachusetts and New York samples also contained multiple private alleles, i.e., alleles observed only in one population. These data strongly suggested that the northeastern USA *P. dominulus* population arose from at least two independent introductions. Johnson and Starks (2004) recommended additional studies to compare native and introduced populations directly.

Here we describe a new genetic study comparing female *P. dominulus* from a native population in central Tuscany, Italy, with four populations in the USA that spanned both the geographic and time scale of colonization: two eastern populations, Massachusetts (MA) and Michigan (MI); and two western populations, northern California (NoCA), and southern California (SoCA) (Table 2). The goals of this study were to compare genetic variation among the native and introduced populations, to test whether the introduced populations have expe-

Table 2. Sampling information from five *P. dominulus* populations used in genetic study.

Year introduced	*N*	Lat. °/Long. °	Location	Collected by
Native	17	43.77 N, 11.25 E	Near Florence, Tuscany, Italy	S. Turillazzi
< 1991*	23	42.56 N, 71.35 W	Great Brook Farm State Park, Carlisle, MA, USA	P. T. Starks
1995	35	42.69 N, 83.12 W	Oakland University campus, Rochester, MI, USA	G. J. Gamboa
2001**	23	37.77 N, 122.22 W	Laney College campus, Oakland, CA, USA	A. E. Liebert
2001	23	34.06 N, 118.44 W	Westwood Village, Los Angeles, CA, USA	P. Nonacs

* Year when fieldwork began at this site, but *P. dominulus* could have been present 3–5 years earlier given the density of nests in 1991. The first Massachusetts report was 26 km east of this site in 1978.

** The date given represents the first sighting at this specific location (P. T. Starks pers. obs.); the initial arrival may have occurred earlier, as *P. dominulus* was observed in the region in 1998.

rienced a genetic bottleneck, and to assess the level of genetic differentiation among introduced populations with the goal of determining whether the USA western populations likely originated from an expansion of the presumably older, eastern introduced populations.

Material and methods

A total of 127 individuals were collected across the five populations, either by netting wasps while they were foraging away from their nests or by collecting wasps at their nests and including one representative per colony matriline to avoid introducing bias caused by overrepresentation of one kin group (*see* Appendix). All wasps were then genotyped at nine microsatellite loci per wasp using primers developed for this species by Henshaw (2000). Protocols were followed as described in Johnson and Starks (2004) and Liebert *et al.* (2004, 2005b) in the International Social Insect Research Facility (ISIRF) at Tufts University.

The microsatellite genotype data were used to calculate measures of genetic variation within populations, to test for the signature of a genetic bottleneck, and to evaluate genetic differentiation across populations. For measures of genetic diversity, the program Genetic Data Analysis (GDA; Lewis & Zaykin 2001) was used to calculate observed and expected percentages of heterozygotes, and FSTAT (Goudet 2001) was used to calculate allelic richness (number of alleles per locus corrected for sample size) for each population. Measures of diversity were compared among populations using the two-tailed paired *t*-test after checking for normality of difference scores.

The program Bottleneck 1.2.02 was used to test whether the introduced populations experienced a genetic bottleneck under the two-phased model (95% strict stepwise mutations, 5% multiple step with variance = 12.00), which is the model recommended for microsatellite data (Piry *et al.* 1999). This program tests for two signatures of recently bottlenecked populations: (1) an excess of heterozygosity relative to the same population under mutation-drift equilibrium, and (2) a mode-shifted allele frequency distribution due to loss of rare alleles (Cornuet & Luikart 1996). As suggested for datasets using fewer than 20 loci, the one-tailed Wilcoxon signed ranks test was used to test for a statistically significant excess of heterozygosity (Piry *et al.* 1999).

Three different measures were used for evaluation of population differentiation. First, the program GDA was used to count the number of private alleles in each population. If more recently introduced populations originated via spreading from older introduced populations, the newer populations should contain only a subset of alleles from the source population. Second, a matrix of F_{ST} values was created (calculated with FSTAT as θ, Weir & Cockerham [1984]) to measure the degree of subpopulation differentiation. Finally, an alternative measure of genetic distance, 1-Psa (proportion of shared alleles), was also used; this may be a more reliable measure of distance than F_{ST} for recently introduced populations that are unlikely to be in equilibrium (Noor *et al.* 2000, Johnson & Starks 2004).

To assess whether western USA populations were likely to have arisen via a secondary founding event originating from the eastern populations, the one-tailed paired *t*-test was used to compare the genetic distance between eastern and western populations *vs.* between the two western populations. The one-tailed test is justified due to the directionality of the hypothesis. A secondary founding event would be revealed as smaller genetic distance (1-Psa) between the western populations than between eastern and western populations.

Results

Of 127 wasps in the sample, all but one were successfully genotyped at a minimum of 8 loci (the remaining individual had genotypes at 7 loci), for an overall genotyping success rate of 98.6% (1127/1143). However, scoring of two loci (Pdom117 and Pdom121) proved difficult to calibrate among populations due to one-base pair differences between many allele sizes. Because of the high risk of scoring errors, these two loci were excluded from further analyses. Probable null alleles were also detected in two loci

(Pdom139, Pdom140) during a different study of the MA population that involved extensive pedigree reconstruction (Liebert & Starks 2006). These two loci were also excluded from analyses unless otherwise noted. Therefore, the majority of analyses were performed using the remaining five loci (Pdom1, Pdom2, Pdom25, Pdom122, and Pdom127b).

Genetic diversity

All nine loci were polymorphic in all populations except for two loci in the SoCA sample (Pdom2, Pdom139). The five populations all contained fairly high levels of genetic variation (Table 3). The native Tuscany population was on average more diverse than each of the introduced populations for all measures (expected % heterozygotes (Nei's 'gene diversity'), observed % heterozygotes, and allelic richness). However, differences in allelic richness between Tuscany and the introduced populations were not statistically significant when the paired *t*-test was corrected for multiple comparisons (required *P* value for statistical significance = 0.005; Tuscany *vs*. MA: $t = 3.17$, $P = 0.03$; Tuscany *vs*. MI: $t = 1.83$, $P = 0.14$; Tuscany *vs*. NoCA: $t = 3.92$, $P = 0.017$; Tuscany *vs*. SoCA: $t = 4.16$, $P = 0.014$; Fig. 1). Allelic richness was similar among the introduced populations (Fig. 1), and did not correlate with population age; the lowest allelic richness values were found for MA and SoCA, which are the oldest and youngest populations, respectively.

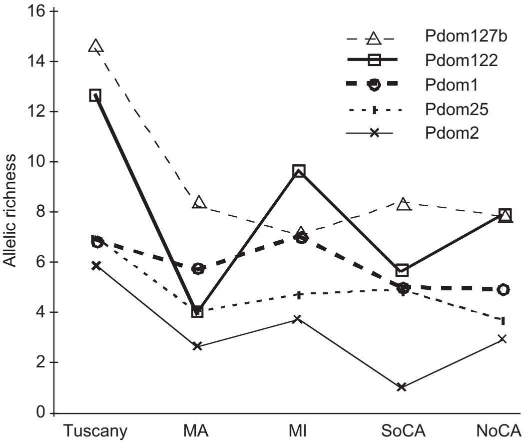

Fig. 1. Allelic richness in native and introduced populations for five microsatellite loci. Abbreviations: MA = Massachusetts; MI = Michigan; SoCA: Southern California; NoCA: Northern California.

Bottleneck tests

None of the introduced populations exhibited the mode-shifted allele frequency distribution expected due to loss of rare alleles after a severe bottleneck. Furthermore, none of the populations were found to have a significant excess of heterozygosity under the two-phased model of mutation. In fact, a significant deficiency of heterozygosity was detected in MI (Wilcoxon signed ranks test: $P = 0.02$). The power of these tests may have been low due to the inclusion of only five loci, especially for SoCA because one locus (Pdom2) was monomorphic and, thus, was not used in the analysis. The data were

Table 3. Multiple measures of genetic diversity of native and introduced *P. dominulus* populations.

Population	*N*	Allelic richness*	Number of private alleles	Expected % heterozygotes	Observed % heterozygotes
Tuscany§	17	9.4	19	77.5	71.1
		10.2	17	76.6	77.9
Massachusetts	23	4.9	0	61.0	52.7
Michigan	35	6.4	3	70.1	68.6
Northern California	23	5.5	1	64.7	71.1
Southern California	23	5.0	6	59.4	58.8

* Calculated by FSTAT, which accounts for differences in sample size among populations.

§ The Tuscany data were reanalyzed excluding Pdom25 due to a probable null allele at this locus for this population only. The top row includes all five loci and the bottom row excludes Pdom25.

reanalyzed including two additional loci with potential null alleles, Pdom139 and Pdom140, but the overall results did not change. Although ideally a minimum of ten loci and 30 individuals per sample should be used for these analyses (Piry *et al.* 1999), the fact that a heterozygosity deficiency was detected in MI suggests that a severe genetic bottleneck is unlikely for at least this introduced population.

Population differentiation

All populations except MA (Table 3) contained private alleles. Tuscany had by far the greatest number of private alleles, which is expected for a native population in comparison with recently introduced populations. However, the distribution of private alleles within the introduced range did not relate to the age of the population: SoCA, the most recently established population, had the greatest number of private alleles (6) followed by MI (5), NoCA (3), and MA, the oldest population, had the fewest.

Two measures of genetic distance, F_{ST} and 1-Psa, were used to evaluate genetic differentiation among populations (Table 4). Based on 120 permutations of the data, all F_{ST} values for introduced population pairs were found to be significantly different from zero ($P = 0.008$; 5% significance level corrected for multiple comparisons with FSTAT), indicating considerable genetic structure across the introduced range. The 1-Psa values were then used to test the probability of a secondary founder event on the west coast originating from eastern source populations. If such secondary spreading did occur, the genetic distance between the two western populations should be lower than the distance between the eastern and western populations. The data did not support such a pattern of spread; in particular, the 1-Psa value between NoCA and SoCA was even higher than that between MI and NoCA (Table 4). The one-tailed, paired *t*-test comparing the genetic distance between NoCA-SoCA with individual east–west population combinations (MA-NoCA, MA-SoCA, MI-NoCA, MI-SoCA) and average differences between the eastern and western populations (MA-Western, MI-Western) did not reveal any significant differences. These data suggest that the two western populations are genetically distinct and did not arise from the same eastern source population.

Discussion

Our results support previous findings by Johnson and Starks (2004) that introduced populations of *P. dominulus* contain relatively high levels of genetic variation and that these populations are the result of multiple introduction events. This is clearly demonstrated by the allelic richness and distribution of private alleles in the introduced populations, as well as the finding that the oldest population, Massachusetts, had the lowest levels of genetic variation. The data also suggest that the sampled western populations did not originate via spreading from the older, introduced eastern populations. The southern California population, in particular, appears to be the most genetically distinct from both the eastern and northern California populations, in addition to possessing the greatest number of alleles not found in the native Tuscany sample. This suggests that the source of the southern California population may be either from an unsampled area within the introduced range, or

Table 4. Two measures of genetic distance between pairs of introduced populations. Above the diagonal: 1-Psa (Proportion of shared alleles, calculated manually; Noor *et al.* [2000]). Below the diagonal: F_{ST} (calculated with FSTAT as θ; Weir & Cockerham [1984]).

	Massachusetts	Michigan	Northern California	Southern California
Massachusetts	*	0.326	0.519	0.561
Michigan	0.047	*	0.324	0.447
Northern California	0.060	0.056	*	0.440
Southern California	0.075	0.085	0.102	*

from a different geographic area from within the native range. Because of frequent shipping between west coast ports and Asian countries, the latter scenario would not be surprising for either southern or northern California.

Evidence shows that multiple independent introductions have contributed to the expansion of the introduced range of *P. dominulus* in North America. However, we still do not know why there have been so many colonization events in the last two decades, since shipping between the native range and North America has been going on long before this period. Perhaps the rate of overseas commerce has increased to such an extent that the probability of an introduction event has also dramatically increased in the last 20 years. The "quality" of transport, such as faster shipping speeds and use of temperature control technologies during transit, may also have increased the survival rates of "stowaway" wasps. It is also possible that introductions did occur prior to the first reported event in Massachusetts, but went undetected either because they experienced local extinction or because populations were only detected when they had expanded after a long time lag. Increased rates of habitat fragmentation, and perhaps increasingly warmer temperatures, may also have made it easier for introduction events to develop into established populations.

We now have evidence that multiple *P. dominulus* populations from different geographical regions of the USA have not experienced severe genetic bottlenecks. Because of the available genetic variation already present, the potential for repeated multiple introductions, and the ability for rapid population increase, this species seems likely to continue its spread throughout North America. Additional large-scale studies of genetic variation are therefore unlikely to provide much further insight into this invasion. Rather, future genetic studies may produce the most interesting results at smaller scales, in regions where newly established populations are expanding into previously uncolonized areas. Such studies may be especially pertinent in locations farther from port cities and thus less likely to experience new introductions; all four sampling locations included in this study were close to shipping ports and thus may have been biased in favor of finding high levels of diversity.

At a smaller geographical scale, information about behaviors such as dispersal, colony foundation, and mate choice may be integrated with population genetic data to gain insight into how new, small populations of *P. dominulus* quickly become established and spread to surrounding areas. Specific questions of interest for future studies involve how genetic variability influences behavioral and life history traits such as finding mates and nest-founding tactics that require the location and recognition of suitable conspecific partners.

For example, the production of diploid males as a result of inbreeding may be a problem for small, colonizing populations of *P. dominulus* if mates are difficult to find. Under normal circumstances, hymenopteran males are haploid and females diploid. This is because of the mechanism of complementary sex determination, in which female development requires a heterozygous genotype at the sex-determining locus. When mates share an allele at this locus, half of the diploid offspring will be homozygous and thus will develop as males. These diploid males are either sterile or produce sterile triploid offspring (reviewed in Liebert *et al.* [2004]). The loss of rare alleles upon introduction may be expected to result in higher rates of such 'matched matings' even without a severe genetic bottleneck (Wares *et al.* 2005). Indeed, diploid male *P. dominulus* have been found in several populations in Massachusetts (Liebert *et al.* 2005b), and triploid females, which are most likely the progeny of diploid males, have also been found in both Massachusetts and Michigan (Liebert *et al.* 2004, 2005b). Diploid male and triploid female production may be most prevalent in small, newly initiated introduced populations where the loss of rare alleles at the sex locus is compounded by inbreeding.

Another example of how behavior may influence or be influenced by genetic diversity relates to colony founding. The typical method of *Polistes* colony foundation in temperate climates consists of one or a small group of females initiating construction of a new nest after emerging from an overwintering period (Reeve 1991). A different approach has been observed during the spring colony-founding phase of *P. dominulus*

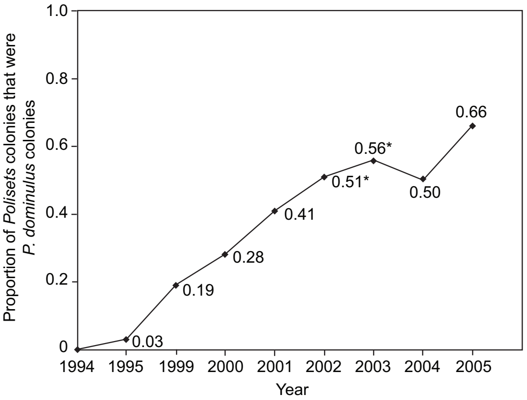

Fig. 2. Proportion of *Polistes* colonies at the Oakland University Preserve that were *P. dominulus* colonies (1994–2005). In 2002 and 2003, large numbers of *P. dominulus* colonies were removed from the Preserve near the end of the colony cycle (denoted with an asterisk).

in New York and southern California, in which massive aggregations of more than 80 wasps have been observed to reuse and expand an old nest (P. T. Starks pers. obs., P. Nonacs pers. comm.). Such unusually large nesting groups could serve to facilitate population expansion in newly colonized areas where individuals may have a difficult time locating conspecifics. If enough genetically unrelated individuals participate in a given nest-founding aggregation, the male and female reproductive offspring produced may be better able to find suitable mates near the nest with reduced risks of inbreeding.

In conclusion, future genetic studies of the *P. dominulus* invasion may be most fruitful in combination with investigations of behavioral and life history traits in introduced populations. Studies of such populations can provide insight into the potential mechanisms for overcoming the initial obstacles to population establishment and expansion.

Successful establishment of *P. dominulus* among native *Polistes* species

As mentioned earlier, one paradox of successful invasion is how a naïve, non-native species is able to outcompete locally adapted native species. North America is home to more than 20 species of *Polistes* wasps (Carpenter 1996a), so the *P. dominulus* invasion provides many opportunities to investigate this question. Where *P. dominulus* has become established in the northeastern USA, *P. fuscatus* had previously been the only common *Polistes* species. Therefore, most of the comparative works to date have examined *P. fuscatus* (Gamboa *et al*. 2002, 2004, Armstrong & Stamp 2003a, Silagi *et al*. 2003). One study also compared *P. dominulus* with the native *P. metricus*, a species found primarily in the midwestern states (Pickett & Wenzel 2000). No such studies have been conducted thus far in the more recently colonized western states. In the following sections, we review these studies, and also provide new, previously unpublished information regarding the comparative biology of *P. fuscatus* and *P. dominulus*.

Displacement of *P. fuscatus* by *P. dominulus* in Michigan

Prior to 1995, *P. fuscatus* was the only species of *Polistes* in Michigan (Owen 1962, West-Eberhard 1969, Gamboa *et al*. 2002). In the spring of 1995, one single-foundress colony of *P. dominulus* was discovered nesting in a *Polistes* nestbox at the Oakland University Preserve in Rochester, Michigan (Judd & Carpenter 1996). The Preserve, which typically contains 60–90 plywood nestboxes, has been used as a *P. fuscatus* research site continuously since 1980. In each subsequent year since *P. dominulus* was discovered in 1995, the proportion of *Polistes* colonies at the Preserve that are *P. dominulus* has increased with the exception of 2004 (Fig. 2).

In the late summer of 2002, approximately a third of the *P. dominulus* colonies at the Preserve were removed because of concern about losing the resident population of *P. fuscatus*. Again in the late summer of 2003, about half of the *P. dominulus* colonies at the Preserve were removed. The removal of *P. dominulus* colonies slowed the proportional increase of *P. dominulus* colonies in 2003 and actually decreased the proportion of colonies that were *P. dominulus* in 2004 (Fig. 2). In 2004, no *P. dominulus* colonies were removed and, as expected, in 2005 the proportion of colonies that were *P. dominulus* increased dramatically (Fig. 2). In 2005, all nestboxes were occupied by *Polistes* and 62 (66%) of 94 colonies at the Preserve were *P. dominulus*. This is the greatest number of *P. dominulus* colonies since their arrival in 1995, and the fewest number of *P. fuscatus* colonies recorded at the Preserve since 1980. The ability to regulate numbers of *P. fuscatus* colonies at this field site by removing colonies of *P. dominulus* clearly demonstrates that there is a causal relationship between *P. dominulus* and the prevalence of *P. fuscatus*.

Gamboa *et al*. (2002) reported that *P. dominulus* had completely replaced *P. fuscatus* in many areas of southeast Michigan. They found that almost all of their former *P. fuscatus* collecting sites now had only *P. dominulus* colonies. Similarly, Silagi *et al*. (2003) reported that by 2000, all of the *P. fuscatus* colonies nesting on the buildings of the 1500-acre Oakland University campus had been replaced by *P. dominulus*. At present, the population of *P. fuscatus* at the Oakland University Preserve is the only *P. fuscatus* population that these authors are aware of in the Detroit metropolitan area (G. Gamboa pers. obs.).

Gamboa *et al*. (2002) found no evidence from extensive videography, field surveys, and field observations that *P. dominulus* was negatively impacting *P. fuscatus* through direct agonistic encounters at the nest. For example in extensive surveys over a two-year period, Gamboa *et al*. (2002) did not record any injured or dead *Polistes* in nestboxes containing colonies of either species. The authors concluded that *P. dominulus* was likely replacing *P. fuscatus* through indirect or exploitative competition, which was consistent with their finding that *P. dominulus* was significantly more productive than *P. fuscatus* (*see* "Colony Productivity" section below). Gamboa *et al*. (2002) suggested that the two species might be competing for nest sites although they acknowledged that other resources might be in short supply.

To examine direct interactions between the two species at nest sites, Silagi *et al*. (2003) videotaped two nestboxes, each of which fortuitously contained a single-foundress colony of *P. dominulus* and a single-foundress colony of *P. fuscatus*. In 12 h of videography, 19 interactions were recorded between the heterospecific foundresses nesting in the same nestbox. All 19 interactions, most of which were aggressive, were initiated by the *P. fuscatus* foundress. In both nestboxes, none of the four colonies produced pupae, and all four foundresses disappeared within several weeks of the videography. The findings of Silagi *et al*. (2003) were consistent with the previous evidence of Gamboa *et al*. (2002) that *P. dominulus* was not replacing the native *P. fuscatus* through direct agonistic encounters.

In summary, current evidence indicates that *P. dominulus* is displacing native *Polistes* in certain areas of the United States and that the displacement is the result of indirect competition. It is not clear what resources are involved in this competition, but suitable nesting sites appear to be the most likely critical resource. The fact that all 90 nestboxes at the Oakland University Preserve are occupied by *Polistes*, and that an increasing number of nestboxes contain two conspecific or heterospecific colonies, is consistent with the hypothesis that *P. dominulus* and *P. fuscatus* are competing for nest sites.

Comparative biology of *P. dominulus* and *P. fuscatus*: why is *P. dominulus* such a successful invader?

Mounting evidence indicates that the introduced *P. dominulus* is displacing *P. fuscatus* in some regions of North America. Various characteristics of *P. dominulus* in its native habitat have been suggested as possible factors contributing to its invasion success, including short development time, aposematic coloration, a generalist diet, and an ability to colonize new environments (*see* Cervo *et al*. 2000). Below we discuss the evidence for these and several additional characteristics as contributing factors to the successful displacement of *P. fuscatus* by *P. dominulus*. We divide these factors into two major categories: (1) productivity and (2) survival. Within each category, we first discuss observed biological differences between species and then consider possible advantages that might result from these differences.

Colony productivity

Polistes dominulus appears to have relatively high colony productivity as compared with sympatric congeners in its native range (Cervo *et al*. 2000). Field observations suggest that in Europe, *P. dominulus* quickly moves into areas and within a few years becomes the predominant *Polistes* species (Cervo *et al*. 2000). In North America, Pickett and Wenzel (2000) reported that in Ohio single-foundress laboratory and field colonies of *P. dominulus* were significantly more productive than comparable colonies of the native *P. metricus*. Gamboa *et al*. (2002) found that in matched comparisons of field colonies in Michigan, single-foundress colonies of *P. dominulus* were 4–5 times as productive at the end of the colony cycle as single-foundress colonies of *P. fuscatus*. The difference in productivity between the two species was significant regardless of whether cell numbers, numbers of cells with meconia, or number of adults on combs were used as estimates of productivity. During the preworker stage of the colony cycle, single-foundress colonies of *P. dominulus* were only about twice as productive as comparable colonies of *P. fuscatus*. However, at about the time of first worker emergence, the productivity of *P. dominulus* increased sharply relative to that of *P. fuscatus* (Gamboa *et al*. 2002).

Gamboa *et al*. (2004) documented that in Michigan both single- and multiple-foundress field colonies of *P. dominulus* were significantly more productive than comparable colonies of *P. fuscatus*. Using both numbers of cells and numbers of cells with meconia at the end of the colony cycle as estimates of productivity, Gamboa *et al*. (2004) reported that single- and multiple-foundress colonies of *P. dominulus* were about 6 and 2.5 times as productive, respectively, as comparable colonies of *P. fuscatus*. The disparity in the productivity of the two species was significantly more pronounced in single-foundress colonies than in multiple-foundress colonies. Interestingly, the rate of multiple colony-founding by the Michigan population of *P. dominulus* has increased since its initial colonization (Gamboa *et al*. unpubl. data), which may influence productivity comparisons in the future. Together, these results provide strong evidence that *P. dominulus* is more productive than the sympatric, native North American *P. fuscatus*.

Timing of colony cycle and duration of brood development

The relatively high productivity of *P. dominulus* may be related to the timing of its colony cycle and brood development. In North America, evidence indicates that *P. dominulus* has a shorter brood development time than native species. Pickett and Wenzel (2000) reported that in single-foundress laboratory colonies, *P. dominulus* produced its first workers earlier than the native *P. metricus*. Similarly, Gamboa *et al*. (2002) found that single-foundress field colonies of *P. dominulus* produced their first workers significantly earlier (approximately 6 days earlier) than comparable field colonies of *P. fuscatus*. The dates of nest initiation were virtually identical in the two species, demonstrating that *P. dominulus* must have shorter brood development times than *P. fuscatus*.

Gamboa *et al*. (2004) compared the timing of colony initiation, first worker emergence, and brood development in both single- and multiple-foundress field colonies of *P. fuscatus* and *P. dominulus*. They again documented that colonies of both species were initiated at the same time in the spring and that *P. dominulus* produced its first workers significantly earlier (approximately 7 days earlier) than *P. fuscatus*. In addition, Gamboa *et al*. (2004) showed that the development times for larvae and pupae, but not eggs, were significantly shorter in *P. dominulus* than in *P. fuscatus*.

The reasons for the shorter brood development in *P. dominulus* as compared with that in other congeners are not presently known. At the mechanistic level, both genetic factors (e.g., smaller adult body size) and environmental influences (e.g., higher provisioning levels) may play a role. Some of the data on foraging patterns and protein allocation described below support the possibility that *P. dominulus* provisions brood with more resources than does *P. fuscatus*. In addition, a possible adaptive hypothesis is that selection pressure exerted by the European *Polistes* social parasites, *P. sulcifer* and *P. seme-*

nowi, favor shorter developmental times in *P. dominulus* (*see* review in Cervo & Dani [1996]). These obligate parasites preferentially attack host nests just prior to worker emergence, and thus host colonies that produce workers quickly may have an advantage. In North America, where *P. dominulus* is free of obligate *Polistes* social parasites, the shortened brood development period could therefore be a preexisting adaptation that has facilitated its invasion success.

Foraging activity patterns

Differences in productivity may also be driven in part by differences in foraging activity. Gamboa *et al*. (2002) compared foraging rates of *P. fuscatus* and *P. dominulus* by observing videotapes of 13 matched sets of single-foundress colonies of both species. In preworker observations, queens of *P. dominulus* made significantly more foraging trips than queens of *P. fuscatus*. Similarly, in postworker colonies, individual workers of *P. dominulus* made significantly more foraging trips than workers of *P. fuscatus*. Thus, both single-foundress queens and workers of *P. dominulus* had significantly greater per-capita foraging rates than queens and workers of *P. fuscatus*.

In 2002 and 2003, a similar study was conducted by videotaping 15 preworker multiple-foundress colonies of *P. fuscatus* and *P. dominulus* at the Oakland University Preserve (127.2 h of observation, 4.24 h/colony). Colonies were matched for date, time of day, spatial proximity, and number of foundresses, and were housed in identical nestboxes that were suspended from the same crossbar one meter apart. *P. dominulus* foundresses made significantly more foraging trips (*P* = 0.001), wood fiber trips (*P* = 0.003), and empty trips (*P* = 0.03) than *P. fuscatus* foundresses. *P. dominulus* foundresses also tended to make more prey trips than *P. fuscatus* foundresses although the difference was not significant (*P* = 0.08, Table 5). The lack of significance for prey trips may be due to low statistical power since prey trips were the least common types of trips (*N* = 8).

The durations of foraging trips in the 15 matched sets of colonies were also compared. *P. dominulus* foundresses made significantly shorter foraging trips (all trips) and wood fiber trips (*P* = 0.009 and *P* = 0.001, respectively) than did *P. fuscatus* foundresses (Table 6). *P. dominulus* foundresses also tended to make shorter prey trips than *P. fuscatus* foundresses (*N* = 8, *P* = 0.06). In summary, foundresses of *P. dominulus* made more and generally shorter trips than foundresses of *P. fuscatus*. The shorter foraging trips of *P. dominulus* may be due to its being a more efficient forager than *P. fuscatus*. Alternatively, the shorter trips of *P. dominulus* may be due to its being less selective in its choice of wood fibers and prey than *P. fuscatus* (Nannoni *et al*. 2001).

Differences in foraging patterns between the species have also been observed during the worker phase. Gamboa *et al*. (2004) found that workers of *P. dominulus* began departing their colony significantly earlier in the day than workers of *P. fuscatus*. This suggests that *P. dominulus* may have a longer foraging day than *P. fuscatus*. However, the authors acknowledged a lack of

Table 5. Numbers of foraging trips (mean ± SD) by foundresses in 15 preworker, matched multiple-foundress colonies of *P. fuscatus* and *P. dominulus* (127.2 h of observation).

Trip type	Number of trips		
	P. fuscatus	*P. dominulus*	*P**
All trips	15.3 ± 10.2	28.5 ± 15.5	0.001
Prey trips	2.5 ± 3.8	5.6 ± 5.2	0.08
Wood trips	6.1 ± 5.8	11.7 ± 7.4	0.003
Empty trips	6.1 ± 4.0	9.1 ± 3.8	0.03

* Two-tailed Wilcoxon matched-pairs test.

Table 6. Duration of foraging trips (mean ± SD) in 15 preworker, matched multiple-foundress colonies of *P. fuscatus* and *P. dominulus* (127.2 h of observation).

Trip type	Duration of trip (sec)		
	P. fuscatus	*P. dominulus*	*P**
All trips	781 ± 359	468 ± 184	0.009
Prey trips	981 ± 398	766 ± 242	0.06
Wood trips	372 ± 159	210 ± 125	0.001
Empty trips	766 ± 561	580 ± 370	0.40

* Two-tailed Wilcoxon matched-pairs test.

data on when the two species terminated their foraging during the day, and thus their hypothesis requires further study.

In a field experiment in which nest site and prey quality and quantity were controlled by use of walk-in cages, Curtis (2005) also found that *P. dominulus* workers foraged more than *P. fuscatus* workers (*P* = 0.002). In addition, compared with *P. dominulus*, *P. fuscatus* foundresses were off the nest more than the average for their workers (*P* = 0.007). Given the risks involved with foraging (Gibo 1978, Reeve & Gamboa 1987), the greater presence of *P. dominulus* foundresses at the nest after offspring emergence may contribute to their success relative to *P. fuscatus*. This difference may also explain the higher queen survivorship in *P. dominulus* reported in Gamboa *et al.* (2002). Additionally, if foundresses actively direct foraging activity of workers as shown by Reeve and Gamboa (1987), differences in foundress presence and behavior could translate into disparities between the species' foraging patterns. Aggression may be the mechanism that foundresses use to regulate foraging activity. Consistent with this idea, Armstrong and Stamp (2003a) found that *P. dominulus* foundresses on the nest were more aggressive toward their offspring than were *P. fuscatus* foundresses, regardless of the density of wasps on the nests.

Use of stored resources

Polistes wasps may meet the energy demands of the colony by means in addition to foraging for prey. One such method is nectar storage. *P. dominulus* and *P. fuscatus* wasps often deposit nectar in some cells, usually a droplet no more than 20% volume of the cell (T. R. Curtis pers. obs.). Silagi *et al.* (2003) reported that preworker *P. dominulus* colonies were significantly more likely to have nectar stored in their combs than *P. fuscatus*. In surveys of 148 colonies (84 *P. dominulus* and 64 *P. fuscatus*) over two years, they also found that *P. dominulus* had significantly more cells containing nectar and a significantly higher proportion of cells containing nectar than *P. fuscatus*. Silagi *et al.* (2003) suggested that nectar storage by *P. dominulus* might provide it an advantage over *P. fuscatus* when climatic conditions prevent foraging. Such an advantage was demonstrated in *P. metricus* by Rossi and Hunt (1988), who showed that nectar supplementation resulted in early production of first offspring and higher percentage of body fat in offspring as compared with controls.

Another use of stored resources is brood sacrifice, in which eggs, larvae and sometimes pupae are fed to other offspring. Previous work shows that *P. fuscatus* nests provided with low levels of prey (low-fed) had similar number of cells but disproportionately fewer cells occupied by immatures than nests in high-fed conditions (Nadeau & Stamp 2003). As expected, foundresses of the low-fed colonies foraged more than those of high-fed colonies. In the low-fed colonies, eggs, which were the first immature stage available for brood sacrifice, were often used to feed offspring. In an experiment that controlled environmental conditions including amount of food, colonies of both species sacrificed similar proportions of immatures, with about 25% to 30% sacrificed (Curtis 2005). However, 48% of immatures sacrificed in *P. dominulus* colonies were eggs, as compared with 14% for *P. fuscatus* colonies (*P* = 0.004). Furthermore, not only was a greater proportion of the *P. fuscatus* sacrificed brood their larvae (*P* = 0.01), but 18% of larvae sacrificed were late instar larvae as compared with 2% for *P. dominulus* (*P* = 0.01). These data are supported by nest-building patterns in the two species. An average of 44% of the cells of *P. dominulus* colonies were half-cells around the periphery of the nest, many of which temporarily held eggs and small larvae. In contrast, *P. fuscatus* nests had significantly fewer half-cells (15%), and most cells were constructed quickly to a size that would support development of pupae (Curtis 2005).

Both species' production schedules likely reflect a strategy of 'no wasted food' (Wenzel & Pickering 1991). Brood sacrifice allows colonies to maintain production during periods of inclement weather and scarce prey. When prey are abundant, colonies may maximize the use of prey via increasing quantity or quality (size) of their offspring, i.e., either many or large mouths to feed. *P. fuscatus* has a longer developmental time than *P. dominulus*; thus, each *P. fuscatus* generation may be exposed to a greater variety of prey quality and quantity as compared with *P. dom-*

inulus. The greater variability of available prey to feed larger-bodied offspring may help explain why *P. fuscatus* is more likely to sacrifice larvae than the faster-developing *P. dominulus*.

Responsiveness to changing resources

Prey availability typically fluctuates throughout the active season of insect predators (Wise 1975, Kasuya 1980, Hurd & Eisenberg 1984, Wiedenmann & O'Neil 1990, Schmid-Hempel & Schmid-Hempel 1998). Armstrong and Stamp (2003a) tested the effects of varying prey quantity on productivity of single-foundress *P. dominulus* and *P. fuscatus* colonies over eight weeks. Nests were placed in wooden boxes (14 × 15.5 × 20 cm) in screen cages (1.8 × 1.8 × 1.8 m) in a field surrounded by woods. When given waxworms (*Galleria mellonella*) ad libitum, both wasp species captured similar amounts of prey and the conversion to total offspring biomass was similar. However, *P. dominulus* is a smaller wasp (Armstrong & Stamp 2003a, Gamboa *et al*. 2004), so although biomass production did not differ significantly between the two species, *P. dominulus* colonies produced approximately 2.5 times the number of workers as did *P. fuscatus* colonies.

In addition, *P. dominulus* were more opportunistic than *P. fuscatus* when prey were abundant (Armstrong & Stamp 2003a). At the end of the experiment, *P. dominulus* colonies given prey ad libitum maintained a high rate of egg-laying and peak numbers of pupae. In contrast, egg-laying and pupal number declined two to three weeks earlier for *P. dominulus* foraging in the field with limited prey available and for *P. fuscatus* with either surplus prey or foraging in the field. These results suggest that *P. dominulus* colonies are more responsive to periods of plentiful prey than *P. fuscatus,* yielding larger colonies by the end of the season.

Another way that the species may differ in their ability to respond to changing resources involves protein allocation. In the construction and maintenance of a nest, *Polistes* wasps use a proteinaceous oral secretion to cement plant fibers together. Approximately 14% of the protein resources gathered during the nest founding stage may be devoted to production of the oral secretion (Kudo *et al*. 1998). The amount of protein allocated to nest construction by paper wasps is positively correlated with exposure to rain (*Ropalidia romandi*, Yamane & Ito [1994]; *Polistes chinensis*, Kudo *et al*. [1998], Kudo [2000]), which suggests that the proteinaceous secretion waterproofs the nest.

Having co-existed with human shelters in Europe for hundreds of years longer than native *Polistes* in North America, *P. dominulus* may use less protein collected from prey to waterproof nests and thus have more protein for provisioning offspring (Pickett & Wenzel 2000). Although *P. fuscatus* may nest in similarly sheltered locations, including man-made cavities, its more recent coexistence with human habitation may make it less able to adjust protein allocation into the nest paper than *P. dominulus*. To test this idea, Curtis *et al*. (2005) experimentally manipulated prey levels in *P. dominulus* and *P. fuscatus* colonies, either giving them a surplus of prey or forcing them to forage on their own. Protein from the nest paper was then extracted using a modified Bradford procedure (Bio-Rad, Richmond, CA). When colonies had surplus prey, protein concentration in the nest paper was relatively high; in contrast, under natural foraging conditions, protein concentration was significantly less (by 43%) for *P. fuscatus* nests and especially so (by 77%) for *P. dominulus* colonies. This suggests that both species are able to adjust protein allocation to the nest according to changes in prey availability. However, *P. dominulus* colonies may have an advantage when prey are limited, because their lower level of protein allocation to the nest may leave more protein available for brood production.

Dietary breadth

Cervo *et al*. (2000) suggested that *P. dominulus* might have a more generalist diet than *P. fuscatus*, thus giving it more flexibility in selection of prey. Such generalist tendencies could reflect (1) an innate ability to locate, handle and/or assimilate prey variety, (2) availability of prey types, and (3) individual and colony learning. A study in Europe by Nannoni *et al*. (2001) found that prey items brought back to nests by *P. domi-*

nulus colonies represented three insect orders. In contrast, North American *Polistes* primarily use caterpillars (Lepidoptera) to feed their offspring (Rabb 1960). No direct comparisons of *P. dominulus* and *P. fuscatus* have been done with respect to breadth of prey items in North America. Nevertheless, two studies on foraging behavior in the two species may shed some light on this hypothesis.

In theory, after locating prey, predators should take prey types in order of preference (Pyke *et al*. 1977). Specialists should show strong preferences, and generalists, for the same energy and time expended, should exhibit weaker preferences (i.e., be less consistent and more opportunistic). Therefore, in an experiment by Curtis (2005) in which both species were given a choice of prey (palatable soft-exterior, unpalatable soft-exterior, palatable hard-exterior and unpalatable hard-exterior), *P. dominulus* was expected to be more of a generalist in its first-prey choice of the day than *P. fuscatus*. Specifically, *P. dominulus* was predicted to (1) exploit a wider array of genera (Cervo *et al*. 2000, Nannoni *et al*. 2001), including soft- and hard-bodied prey, and/or (2) exhibit a weaker preference (i.e., more opportunistic response; Armstrong & Stamp [2003a, 2003b]). However, there was no difference between the wasp species; both *P. dominulus* and *P. fuscatus* significantly preferred as their first choice of the day the palatable soft-exterior prey. The wasps rejected the other prey types in similar proportions, but once the palatable soft-exterior prey were taken, both species most often chose the unpalatable soft-exterior prey.

These results suggest that *P. dominulus* may not routinely be more of a generalist than *P. fuscatus*. However, in this experiment, moderate amounts of prey were available. It is possible that *P. dominulus* may be more of a generalist than *P. fuscatus* under conditions of prey scarcity, similar to the previous experiment where *P. dominulus* exhibited opportunistic behavior (Armstrong & Stamp 2003a). Under such conditions, we would also expect differences between the species in protein allocation to the nest and in brood sacrifice.

Although Weiss *et al*. (2004) did not test the dietary breadth hypothesis, their comparison of *P. dominulus* and *P. fuscatus* learning to deal with shelter-building caterpillars is instructive. If *P. dominulus* is inherently more of a dietary generalist, an expectation might be that it can better handle novel foraging situations or learn more quickly. However, the data do not support that. For example, 81% of previously naïve *P. fuscatus* given a context experience (caterpillars standing on the outside of their shelter) subsequently removed a caterpillar from a shelter, whereas 57% of *P. dominulus* did so. In terms of searching and handling, behavior and time spent by the wasp species were similar.

So based on studies to date, the hypothesis that *P. dominulus*' success may be due in part to it being more of a dietary generalist than other *Polistes* is unsupported. Given that under natural conditions foraging is risky, prey availability is often unpredictable, and extra prey tissue cannot be stored (Strassmann *et al*. 1984), it is likely that these factors have selected for a strategy of "no wasted food" in *Polistes* wasps (Wenzel & Pickering 1991) as mentioned previously regarding brood sacrifice patterns. This strategy may explain why wasps do not completely avoid non-preferred prey types when they are encountered (Stamp & Meyerhoefer 2004). It may also explain the reports suggesting that *P. dominulus* takes a wider variety of prey than other *Polistes* species (Nannoni *et al*. 2001). Individual *P. dominulus* facing the same conditions as *P. fuscatus* may not be more of a dietary generalist; rather, the response of *P. dominulus* colonies may be more opportunistic relative to resources, for example, via more workers foraging and thus better canvassing of an area. Other opportunistic behaviors by *P. dominulus*, including the use of eggs held in numerous half-cells to feed offspring and the reduced allocation of protein to nest construction, would allow colonies to take advantage of poorer quality prey during periods of low prey availability. But it is not clear whether these opportunistic provisioning behaviors of *P. dominulus* are primarily advantageous where human-altered environments affect prey type and availability.

Colony survival

Polistes colonies may fail for a variety of reasons, including loss of the entire nest and brood to predation or parasitism, or loss of foundresses in the preworker phase. Foundresses may also be usurped by conspecifics during the preworker phase, and thus be prevented from producing their own reproductive offspring. Gamboa *et al.* (2002) reported that single-foundress queens of *P. dominulus* had a significantly greater survivorship than single-foundress queens of *P. fuscatus*. Furthermore, queen longevity in both species was positively correlated with colony productivity. For *P. fuscatus*, the correlation was highly significant ($P < 0.01$). Due to the complexities of the *Polistes* colony cycle, it is difficult to categorize colonies as absolutely surviving or failing; for example, wasps may renest after a predation event, and parasitism or usurpation may result in only a partial loss of brood. We therefore review evidence for differences in the susceptibility of *P. dominulus vs. P. fuscatus* to a variety of forces impacting colony survival.

Nest usurpation

Gamboa *et al.* (2002) did not observe any attempted or successful usurpations of either conspecific or heterospecific colonies by *P. dominulus* foundresses at the Oakland University Preserve. In contrast, the authors observed numerous attempted conspecific and heterospecific usurpations as well as successful conspecific usurpations by foundresses of *P. fuscatus*.

Since Gamboa *et al.* (2002) had relatively small sample sizes that did not lend themselves to statistical comparisons, Gamboa *et al.* (2004) reexamined usurpation in *P. fuscatus* and *P. dominulus* by videotaping matched, multiple- and single-foundress colonies of both species. They observed 69 conspecific usurpation attempts by foundresses of which 61 were by *P. fuscatus* and 8 by *P. dominulus* ($P < 0.001$). Colonies of *P. fuscatus* also experienced significantly more usurpation attempts than did *P. dominulus* colonies. Thus, *P. fuscatus* was more likely to attempt usurpations, and its colonies experienced more usurpation attempts, than *P. dominulus*.

Polistes fuscatus, like *P. metricus* (Gamboa 1978), is known to have high conspecific usurpation pressures. Gamboa *et al.* (1992) reported that, on average, a colony of *P. fuscatus* experienced one usurpation attempt per day. Most successful usurpations in *P. fuscatus* and *P. metricus* occur in single-foundress colonies, presumably because single-foundress colonies are left unattended more often and for longer periods of time than multiple-foundress colonies (Gamboa 1978, reviewed in Reeve 1991, Gamboa *et al.* 1992). Gamboa and Stump (1996) documented that foundresses of multiple-foundress *P. fuscatus* colonies coordinate their foraging, which reduces the time nests are left unattended, presumably in response to high conspecific usurpation pressures.

Unlike *P. fuscatus* and *P. metricus*, *P. dominulus* has rarely been observed to engage in either conspecific or heterospecific usurpation in its native range (Gamboa *et al.* 2004). If *P. dominulus* has evolved in habitats lacking strong usurpation pressures, we would expect foundresses of *P. dominulus* to be less likely to coordinate their foraging and minimize nest inattendance. In order to examine this, the number of times and the proportion of time that nests of *P. fuscatus* and *P. dominulus* were unattended were recorded in 15 matched, preworker multiple-foundress colonies at the Oakland University Preserve. In 127.2 h of two-hour observations, *P. dominulus* colonies were unattended significantly more often (mean ± SD = 5.1 ± 5.8 times/observation, $P = 0.04$) than colonies of *P. fuscatus* (mean ± SD = 1.0 ± 1.6 times/observation). Similarly, *P. dominulus* colonies were unattended a significantly greater proportion of the observation time (mean ± SD = 0.044 ± 0.047, $P = 0.03$) than colonies of *P. fuscatus* (mean ± SD = 0.01 ± 0.017, two-tailed Wilcoxon matched-pairs test for both comparisons). Foundresses of *P. fuscatus* and *P. dominulus* did not spend different amounts of time away from the nest ($P = 0.09$, two-tailed Wilcoxon matched-pairs test), and thus the differences in nest inattendance cannot be attributed to differences between the species in time away from the nest. The large disparity in productivity between single-foundress colonies of *P. dominulus* and *P. fuscatus* may be at least partly due to the intense conspecific usurpation pressures experienced by *P. fuscatus*, but not by *P. dominulus* single foundresses. Similarly, the significantly higher survivorship or longevity documented in single foundresses of *P. dominu-*

lus (Gamboa *et al*. 2002) may be partly due to its lack of usurpation pressures and its tendency to store nectar in preworker combs.

Parasitism

In North America, native *Polistes* are subject to several different parasites and parasitoids (Nelson 1968). Introduced *P. dominulus* populations are not completely free from these pressures, as we have observed colonies filled with slanted webbing that is characteristic of pyralid moth infestation (Massachusetts: A. E. Liebert & P. T. Starks pers. obs., Utah: S. Turillazzi pers. obs.) No studies have yet addressed the overall frequency of parasitism of the two species. However, some authors have suggested that introduced *P. dominulus* populations may have an advantage over native populations due to release from the pressures of Strepsipteran parasites (Cervo *et al*. 2000, Pickett & Wenzel 2000), which frequently attack this species in its native range (Hughes *et al*. 2003, 2004a, 2004b).

Pickett and Wenzel (2000) collected colonies of *P. dominulus* and *P. fuscatus* from New York state and reported that only *P. fuscatus* was parasitized by Strepsipteran parasites. Similarly, Gamboa *et al*. (2004) recorded Strepsipteran parasites in 11 of 28 colonies of *P. fuscatus*, but in none of the 30 colonies of *P. dominulus* in surveys at the Oakland University Preserve in Michigan. These results suggested that the Strepsipteran parasites were host specific for the native species of *Polistes*, and that *P. fuscatus* was at a disadvantage relative to *P. dominulus* with respect to Strepsipteran parasites (Gamboa *et al*. 2004). The latter conclusion, however, may be premature. In general, parasitism by Strepsipterans can be difficult to detect in *P. dominulus* since female parasites are cryptically hidden between host tergites and sternites (Hughes *et al*. 2003). In addition, Hughes *et al*. (2004b) recently reported that in Europe female *P. dominulus* parasitized by Strepsipteran parasites desert their colony and form large aggregations near male lek sites. Thus, parasitized females of *P. dominulus* may escape detection in surveys of colonies. It is possible that the *P. dominulus* introduced into North America brought with them native Strepsipteran parasites and that these cryptoparasitic Strepsiptera have gone undetected by North American researchers. Further comparative studies of parasite and parasitoid pressures on *P. dominulus vs*. native species are needed to address this question.

Predation

Polistes wasps are known to have a number of vertebrate predators including raccoons and birds. However, *P. dominulus* may suffer less nest predation than other *Polistes* (Cervo *et al*. 2000). Studies in Europe indicate that *P. dominulus* has less nest predation by birds than do other sympatric wasp species (Dani & Cervo 1992). Cervo *et al*. (2000) suggested that this difference might reflect the aposematic coloration of *P. dominulus* and/or the tendency for *P. dominulus* to nest in more sheltered sites than other species. In addition to these factors, the behavior of the wasps when threatened and the strength of the comb's attachment to the substrate may also influence relative rates of predation.

The likelihood of being attacked by vertebrate predators may depend in part on the appearance and behavior of the wasps when they are threatened. *P. dominulus* and *P. fuscatus* wasps differ greatly in their coloration patterns and to some degree in their behavior. In the northern end of its range, *P. fuscatus* is a cryptically-colored brown wasp with a few faint, thin yellow bands. In contrast, *P. dominulus* is bright yellow alternating with black, similar to the warning coloration of *Vespula germanica*, a common and aggressive yellowjacket (Cervo *et al*. 2000). The aposematic coloration of *P. dominulus* may be sufficiently effective in deterring diurnal vertebrate predators that leaving the nest to attack, which is risky (Reeve & Gamboa 1987), may be unnecessary.

P. dominulus may therefore have less need than *P. fuscatus* for behavioral responses to vertebrate predators, including humans with whom they often live in close association (Judd & Carpenter 1996). Curtis and Stamp (2006) tested this idea by measuring the response of the two species to humans approaching the nest, starting at 1.75 m from the nest and then moving closer by intervals of 0.5 m. Defensive behavior of *P. dominulus* and *P. fuscatus* at the nest towards vertebrates was categorized into four levels, ranging from most to least tolerant: A level one response consisted of the wasp turning to face the intruder with its wings in their resting position. A level two response consisted of the wasp facing the intruder while raising its body and spreading the wings at about a 45-degree angle. A level three response consisted of the wasp beating its wings rapidly while grasping the nest with its legs and causing a buzzing sound. A level four response consisted of the wasp flying from the nest to attack and sting the intruder. Interestingly, during the level three buzzing response, *P. fuscatus* always turned to face the intruder; in contrast, *P. dominulus* always turned away from the intruder, showing its aposematically colored abdomen. The mean response level data were analyzed using repeated measures ANOVA.

The results of this experiment showed significant differences between the species in their tolerance of human approach. About the time that workers began emerging, *P. fuscatus* foundresses became less tolerant of humans than *P. dominulus* foundresses and remained so for the rest of the summer ($P = 0.002$). Furthermore, *P. fuscatus* foundresses were less tolerant of humans approaching the nest than *P. fuscatus* workers, which exhibited a similar response level to that of *P. dominulus* workers and foundresses (statistical interaction of factors with $P = 0.02$). Consequently, with a human approaching the nest, *P. dominulus* foundresses and workers were significantly less likely to leave the nest and attack than were *P. fuscatus* foundresses. The greater nest affinity of *P. dominulus* foundresses when disturbed relative to *P. fuscatus* foundresses may be related to the behavioral display of aposematic coloration that would make a higher-level response unnecessary. Since worker nest affinities did not differ between the species, this difference may be most relevant to the preworker phase when only foundresses are present.

Gibo (1978) reported that several species of birds, including Baltimore orioles and blue jays, are predators of paper wasps. Silagi *et al*. (2003) suggested that *P. dominulus* might have an advantage over *P. fuscatus* against avian predators because their combs might be more strongly attached to the substrate than combs of *P. fuscatus*. The authors were led to this hypothesis by their finding that *P. dominulus* had a significantly greater number of pedicels per comb and per cell than *P. fuscatus*, possibly resulting in a stronger attachment of the comb to the substrate. Consistent with this hypothesis, Silagi *et al*. (2003) observed that over a period of several years, colonies of *P. fuscatus* were more quickly replaced by *P. dominulus* when colonies were *not* protected from birds.

To test the hypothesis of Silagi *et al*. (2003), the strength of attachment of combs was compared in a study of the two species. In 2004 after the end of the colony cycle, 22 plywood nestboxes containing empty *P. fuscatus* combs and 22 nestboxes containing empty *P. dominulus* combs were collected from the Oakland University Preserve in Rochester, Michigan. The 44 nestboxes were grouped into 22 pairs that were matched for cell number, each pair consisting of one *P. fuscatus* comb and a similar sized *P. dominulus* comb. For 11 matched pairs, the lateral "force" (pulling motion perpendicular to the alignment of the pedicel) required to dislodge the combs was recorded, and for another 11 matched pairs, the downward "force" (a pulling motion in alignment with the pedicel) required to dislodge the combs was recorded. In order to measure the strength of attachment of combs, 0.5 cm wide ribbons were placed around the combs, then the ribbons were attached to a Chatillon spring scale and pulled until the comb was dislodged. A Sony Hi8 camcorder with a 15 cm diameter field of view was used to film the procedure, focusing on the gradations of the scale to more precisely measure the maximum deflection of the scale (in grams) prior to the dislodgment of the combs. Measurements were recorded blindly for each comb, i.e., the observer did not know which species was being tested.

For lateral "force" measurements, which simulated attacks from birds, combs of *P. dominulus* were significantly more strongly attached than combs of *P. fuscatus* ($P = 0.03$, mean ± SD = 1231 ± 1018 *vs*. 570 ± 415 g, respectively). Surprisingly, for downward force measurements, the strength of attachment of *P. fuscatus* and *P. dominulus* combs was not significantly different ($P = 0.13$, mean ± SD = 427 ± 305 *vs*. 551

± 387g, respectively). In addition, there were significant, positive correlations between the size of the comb (number of cells per comb) and the strength of attachment of the comb (lateral force) for *P. fuscatus* (Spearman rank correlation: $r = 0.682$, $P = 0.02$) and *P. dominulus* (Spearman rank correlation: $r = 0.867$, $P = 0.0006$). Thus, for both species, larger combs were more strongly attached to the substrate than smaller combs. Since combs of *P. dominulus* are 2 to 6 times larger than combs of *P. fuscatus* at comparable times during the colony cycle (Gamboa *et al.* 2004), the disparity in the strength of attachment (lateral force) between the species is likely to be even more pronounced than the reported values for colonies matched for cell number. Birds are known to fly at paper wasp nests from the side, knock them to the ground, and consume the contents of the cells (Rau 1941, Gibo 1978, Noonan 1979, G. Gamboa pers. obs.). Therefore, *P. dominulus* combs may less likely be dislodged from their substrate by birds than *P. fuscatus* combs because the side force required to dislodge combs is greater for *P. dominulus* than *P. fuscatus*.

Differences in colony survival may also depend on the ability of wasps to renest after a predation event. Gamboa *et al.* (2004) reported that in 2001 raccoons destroyed large numbers of both *P. fuscatus* and *P. dominulus* colonies nesting in plywood boxes at the Oakland University Preserve. After the attack by raccoons, the authors documented that *P. dominulus* colonies were significantly more likely to reconstruct their nests than *P. fuscatus* colonies. More specifically, 11 of 19 *P. dominulus* colonies but only 1 of 23 *P. fuscatus* colonies renested after being destroyed by raccoons. A comparison of renesting frequencies in large and small colonies revealed that the greater likelihood of renesting by *P. dominulus* was not due to the larger sizes of their colonies. Most colonies of *P. dominulus* that renested were successful, i.e., they subsequently produced adults. Thus, *P. dominulus* had a productivity and survivorship advantage over *P. fuscatus* after raccoon predation. The greater tendency of *P. dominulus* colonies to renest after raccoon predation may be related to their shorter brood development times. That is, *P. dominulus*, but not *P. fuscatus*, may have had sufficient time to successfully renest after the destruction of their original nest.

In summary, *P. dominulus* appears to have advantages over *P. fuscatus* with respect to both mammalian and avian predators. Specifically, *P. dominulus* colonies have a significantly higher probability of successfully renesting after raccoon predation, the display of aposematic coloration by *P. dominulus* may result in fewer attacks by vertebrates and less need for nest defense in preworker colonies, and *P. dominulus* combs may be more difficult to dislodge by avian predators than those of *P. fuscatus*.

Winter survivorship of gynes

Larger female terrestrial arthropods may have a better chance of surviving the winter than smaller female arthropods (Wise 1975). Given their difference in size, *P. fuscatus* may have higher overwintering success than the smaller *P. dominulus*. Although *P. fuscatus* can withstand temperatures as low as –15 °C (Gibo 1972) and appears to be “sufficiently cold hardy to survive nearly complete exposure to the midwinter temperature regime of southern Ontario” (Gibo 1980a), typically only 10% of *P. fuscatus* reproductive females survive winter (Gamboa *et al.* 1991). Even so, this may be a higher survival percentage than that of the smaller *P. dominulus*.

Gamboa *et al.* (2004) marked 1871 fall gynes (497 *P. fuscatus* and 1374 *P. dominulus*) with colony-specific colors and recorded the presence and locations of these colony-marked foundresses the following spring. Of 66 colony-marked spring foundresses, 41 (26 colonies) were *P. fuscatus* and only 25 (18 colonies) were *P. dominulus*. The number of colony-marked foundresses of *P. dominulus* was significantly less than expected, indicating that gynes of *P. dominulus* had suffered significantly greater mortality during winter diapause than *P. fuscatus*. It is possible that differential dispersal rather than mortality could account for these differences; however, surveys of buildings up to a mile from the research site revealed no colony-marked foundresses of either species. In addition, Gamboa *et al.* (2004) measured the distance between each colony-marked foundresses’ natal site and the site of its spring colony. Both species were equally, strongly philopatric and nearly half of all colonies initiated spring colonies within a meter of the site of their natal colony (Gamboa *et al*. 2004). Although *P. dominulus* foundresses tended to nest closer to their natal sites than *P. fuscatus* foundresses, the difference was not significant. Thus, the differences in winter survivorship between the species in this study are unlikely to be due to greater dispersal by *P. dominulus*.

Conclusions

Polistes dominulus has an enormous advantage over the native congeners in its introduced range in both colony productivity and survival. Multiple characteristics of *P. dominulus* are likely to contribute to its high productivity, including earlier production of workers, greater nectar storage, higher queen and worker foraging rates, and a greater ability to respond to changing resource levels. Colony failure rates may also be relatively lower in *P. dominulus* than *P. fuscatus* because of the former's lower usurpation pressures, higher survivorship of single-foundress queens during the active season and ability to better tolerate predation by raccoons and possibly birds. Additional possible advantages of *P. dominulus* over *P. fuscatus* may include decreased predation risk due to aposematic coloration, more efficient foraging, and reduced vulnerability to Strepsipteran parasites.

The only aspect of the biology of *P. fuscatus* that has been shown to provide it an advantage over *P. dominulus* is its substantially higher survivorship during winter diapause. It is not clear why *P. dominulus* gynes had such poor winter survivorship relative to gynes of *P. fuscatus*. *P. fuscatus* is larger than *P. dominulus* and, in invertebrates, typically larger size is correlated with higher survivorship (Wise 1975). *P. fuscatus* may also have disproportionately greater fat stores or greater cold tolerance than *P. dominulus*. If so, we would expect *P. dominulus* to be relatively less successful in higher latitudes of North America, particularly those latitudes that are near the northern limits of the range of *P. fuscatus*. Alternatively, it may be that *P. fuscatus* is better able to locate suitable hibernaculae than *P. dominulus*. In any event, the relatively poor survivorship of *P. dominulus* gynes during winter diapause undoubtedly partly counters its tremendous productivity advantage over *P. fuscatus*.

The relative importance of the biological factors described above may differ depending on environmental conditions and the particular native species that are sympatric with *P. dominulus*. Climatic differences in the introduced range might be a factor that influences the advantages of *P. dominulus* over native congeners. For example, there is generally no rainfall during the nesting period of paper wasps in southern California. Thus, the native species (*P. aurifer*) in this region would not be expected to differ from *P. dominulus* in the allocation of protein to nest paper. Similarly, species such as *P. carolina* that generally nest in natural cavities (Rau 1929, Seppä *et al*. 2002) would not be expected to differ from *P. dominulus* in this regard. Many *Polistes* species native to North America are well adapted to suburban and rural environments, but *P. dominulus* may be especially well adapted to such human-modified habitats. It remains to be documented whether *P. dominulus* has become established mainly or exclusively in these areas throughout its introduced range.

In its native range, *P. dominulus* is sympatric with multiple congeners, including obligate social parasites. This competitive environment may have favored the selection of traits leading to the extremely high productivity and survivorship in this species, and its subsequent success as an invasive species. Interestingly, *P. dominulus* has thus far not been reported in the southeastern USA, perhaps because of the higher diversity of native *Polistes* in this region. These native *Polistes* may have evolved in a competitive environment similar to that of *P. dominulus* in its native range. If *P. dominulus* eventually colonizes the southeastern USA, it may be less likely to dominate the resident species as it has done with *P. fuscatus* in the northeast.

Overall, the pattern of the *P. dominulus* invasion is similar to that of other successful introduced species. *P. dominulus* is highly productive relative to native, sympatric *Polistes*. It is associated with and tolerant of humans and a human-altered landscape. It is opportunistic, as demonstrated by its nest placement and response to prey availability. In areas where it has invaded, it appears to suffer less vertebrate predation and/or parasitism than native *Polistes*. Together, these characteristics suggest that once *P. dominulus* becomes established in human-modified habitats, it is likely to become a permanent, abundant and trophically important member of the plant–insect community.

Ecological impacts of *P. dominulus* in its introduced range

Along with other highly invasive species, *P. dominulus* is becoming a cosmopolitan species. The fate of native *Polistes* sympatric with *P. dominulus* is less clear, but it will no doubt be shaped greatly by how humans are modifying the environment. Below we discuss the potential ecological impact of *P. dominulus* in North America, focusing on the role played by human effects on the environment including patterns of conservation of biological control agents, increasing habitat fragmentation, and warmer conditions in urban-suburban areas and regionally due to global warming.

Polistes wasps are ecologically important because of their role in controlling caterpillars, which are major herbivores in natural, agricultural and forestry ecosystems (Rabb & Lawson 1957, Lawson *et al*. 1961, Gillaspy 1979, Gould & Jeanne 1984). Consequently, *Polistes* wasps have been used to control caterpillar pests, although their use as biological control agents has had mixed success (Furuta 1983, Gould & Jeanne 1984). This may reflect the need for management that is specific to particular situations (Raveret Richter 2000). Nonetheless, *P. dominulus* may be a better biocontrol agent than other *Polistes*. The same characteristics that make it a successful invader would be advantageous in a biocontrol agent, i.e., a high rate of productivity, tolerance of humans and human-modified landscape, opportunistic response to prey availability, and low rates of parasitism and predation.

It is thought that conservation and augmentation of insect predators may preclude invasion by exotic pests and maintain pest-free zones (Ehler 1998). Conservation biological control (i.e., conservation of species that provide control of others that could become pests) is crucial as (1) the number of introduced species (and thus the pool of potential pests) increases, and (2) the area of human-modified habitat increases (which favors establishment and proliferation of introduced species) (Landis *et al*. 2000). Introduced insect predators have the potential to displace native predators, but they may also provide less effective biological control of insect pests especially if the introduced predators are generalist feeders (Elliott *et al*. 1996). The introduction of *P. dominulus* is an interesting case because it is unclear whether it has completely displaced native *Polistes* in some areas, or only appears to have done so because populations are concentrated in human-altered habitats where colonies are more easily located and studied (e.g., Judd & Carpenter 1996).

Habitat fragmentation and the subsequent creation of a matrix of urban, suburban, rural and natural habitats are likely to affect the distribution and abundance of *Polistes* species. Recent literature on conservation of biological control agents (native and introduced) has called for a better understanding of the distribution and abundance of such agents across the landscape and the factors that shape these patterns (Ferro & McNeil 1998, Letourneau 1998, Symondson *et al*. 2002). It may be that *P. fuscatus* fares better than *P. dominulus* in natural habitats where nest sites are branches and rock ledges and crypticity is advantageous. However, as habitat fragmentation continues, there may be fewer natural areas large enough for *P. fuscatus* populations to thrive. Given its proclivity for human-modified habitats, *P. dominulus* may actually be better suited than other *Polistes* as a biological control agent in an altered landscape consisting of patches of urban, suburban, rural and no-longer-pristine natural ecosystems. Furthermore, some human-modified habitats may serve as a population source for some insect predators, but as a population sink for others (Taylor *et al*. 1993). For example, suburban areas may serve as a source of *P. dominulus*; in contrast, human-modified woodlands may serve as a sink for *P. dominulus* but as a source for *P. fuscatus*. Evaluating such situations and then developing optimal management is one of the challenges of urban ecology. In particular, studies are needed to document the relative success of *P. dominulus* and native *Polistes* in natural *vs*. human-disturbed landscapes in order to determine where and in what ways *P. dominulus* is likely to have the greatest ecological impact.

Although we do not have comparative data to examine the hypothesis that warmer temperatures (as with global warming or in suburban–urban areas) favor *P. dominulus* over *P. fuscatus,* it seems plausible based on the recent range expansion of *P. dominulus* into higher latitudes. In addition to the disproportionately greater effect of global warming on higher latitudes (IPCC 1996, 2001), urban–suburban areas tend to be warmer than adjacent rural or natural sites (von Stulpnagel *et al*. 1990), and nests on or in buildings are likely to be warmer than those in bushes or trees. Moreover, in urban–suburban areas, nighttime temperatures are higher, and small green areas (one hectare or less) can have their own microclimates (von Stulpnagel *et al.* 1990). As a result, arthropod densities in northern European cities can be similar to those of southern rural areas (Tischler 1973); both wasp and prey densities are likely to exhibit these patterns. Warmer conditions are expected to affect the spread and impact of introduced species (Simberloff 2000). Indeed, it is these warmer situations where introduced *P. dominulus* seems often to gain its initial foothold.

Some experiments with *P. fuscatus* shed light on the effect of nest temperature on productivity. Using a modification of Jeanne and Morgan's (1992) procedure, nest box temperature at outdoor sites was altered by placing either a white styrofoam cover or a black cloth cover on nestboxes, with temperature recorded by data recorders in the boxes. When both prey quantity and nest box temperature were manipulated, high-fed warm-nest-box colonies produced about 60% more offspring than that of the other treatments (high-fed and cool, low-fed and warm, low-fed and cool), which produced numbers of offspring similar to each other (interaction term $P = 0.04$ followed by multiple comparison tests, Nadeau & Stamp 2003). The daily average difference of 1.3 °C between the warm and cool nest boxes was significant ($P = 0.001$). Importantly, this difference is within the range expected due to global warming over the next 50 years (IPCC 1996, 2001) and, thus, illustrates that what might seem a relatively small difference can have a large ecological effect. The results from this experiment suggest that well-fed colonies nesting on or in human shelters in urban–suburban areas are likely to be much more productive. Although *P. fuscatus* can benefit by such warmer nest sites, *P. dominulus* is invading areas at the expense of *P. fuscatus*. Thus, with the demise of *P. fuscatus* in such areas, *P. dominulus* will accrue the benefit of warmer nest sites in human-modified habitats.

The introduction of *P. dominulus* may also have indirect effects on some cavity-nesting birds, which may find themselves in competition with *P. dominulus* for nest sites. Gibo (1980b) found evidence for such competition between *P. fuscatus* and house wrens *Troglodytes aedon* in Ontario, Canada; in that study, the aggressive male wrens actually destroyed small *P. fuscatus* colonies and filled nestboxes with twigs, which prevented their use by wasps. Less aggressive cavity-nesting bird species may not fare so well as house wrens, however, and the short brood development time and high productivity of *P. dominulus* may give this species an advantage in such competition as compared with *P. fuscatus*, as birds typically attack nests prior to the worker phase (Gibo 1978). *P. dominulus* also may be more likely to find suitable nest-building substrate in cavities already containing nesting birds because it is significantly more likely to build nests on vertical surfaces as compared with *P. fuscatus* (Silagi *et al*. 2003). This could be especially relevant for attempts by people to attract declining species of native cavity-nesting birds, such as the eastern bluebird, to suburban habitat by putting out nestboxes. Non-native cavity-nesting birds such as house sparrows and European starlings already provide competition with native birds for these suburban nestboxes, and the effects of *P. dominulus* on this competition remain to be seen.

In sum, if *P. dominulus* proves to be a competent biological control agent across a matrix of human-modified habitats, this may counter the usual role of a cosmopolitan introduced species as a "weedy-species" contributing to a decline of native biodiversity. However, whether the potential biocontrol advantages of the *P. dominulus* invasion of North America will outweigh its disadvantages remains an unanswered question.

P. dominulus as a model system for invasion biology

The behavioral plasticity of primitively eusocial societies may allow *Polistes* species to be particularly successful invaders. Perhaps not surprisingly, *P. dominulus* is not the only successful invader out of over 206 species in this cosmopolitan genus (Reeve 1991, Carpenter 1996b). The neotropical *P. versicolor* has become established in the Galápagos Islands after its introduction in 1988, presumably in a shipment of bananas (Roque-Albelo & Causton 1999), and *P. chinensis* is currently spreading throughout New Zealand after being introduced from Japan in 1979 (Clapperton *et al*. 1996). Research on these invasions is only beginning to address the specific reasons for their success and place these findings within the larger context of invasion biology.

A thorough investigation of introduced species must incorporate ecological, behavioral, life history and population genetic data (Holway & Suarez 1999, Lee 2002). The status of the *Polistes* genus as a model system for behavioral and evolutionary studies (Reeve 1991, Gamboa 1996, Queller *et al*. 2000, Dani *et al*. 2001) provides a unique advantage for research into the causes and consequences of *Polistes* species invasions. Study of the *P. dominulus* invasion is particularly worthwhile because of the opportunity to combine new population genetic, behavioral and ecological data in the introduced range with a long tradition of behavioral research on this species in its native Europe. In fact, early work on *Polistes* behavior began with European *P. dominulus* in the 1940s (e.g., Pardi 1948), and behavioral research with *P. dominulus* remains active in Europe (e.g., Italy: Dapporto *et al*. [2004, 2005], France: Mead & Pratte [2002], Spain: Shreeves *et al*. [2003]). Fortuitously, the North American species *P. fuscatus* also has a long history of behavioral study, beginning with Owen (1962), West-Eberhard (1967, 1969) and Noonan (1979). Such in-depth knowledge of the behavior of both *P. dominulus* and *P. fuscatus* in their native habitats prior to the North American introduction of *P. dominulus* will facilitate future work on this invasion. We are also fortunate in beginning to study this invasion early enough to examine the spread of *P. dominulus* as it becomes sympatric with multiple native North American *Polistes* species. This timing permits comparative studies of the invasive and native species in the same habitat, and allows us to examine competitive interactions directly as they occur.

Just as primitively eusocial insects are used as a model system for understanding the transition from solitary living to eusociality, the study of the *P. dominulus* invasion could similarly serve as a model system for further understanding the invasion biology of a broad range of introduced species. For example, studies such as those reviewed here may help explain why the *P. dominulus* invasion seems to be occurring more rapidly than previous North American invasions by the European social wasps *Vespa crabro* and *Vespula germanica*. *Polistes* may be an especially useful model system to contrast with other widely studied invasive species such as fire ants and Argentine ants. Although ant invasions are interesting and important areas of study, the advanced eusocial organization of ants makes them less suitable models for providing insight into invasions of species with more flexible social systems.

Polistes wasps, with their flexible social systems, may allow research on the *P. dominulus* invasion to be more broadly applied to social systems including subsocial, semisocial, and primitively eusocial species, as well as for comparison with solitary taxa. The status of *Polistes* wasps as ecologically important predators of agriculturally relevant prey species and the potential for negative impacts of increasing *P. dominulus* populations on native birds and insects means that research on this invasion has implications for biocontrol programs and management of native species. In addition, the ability of *P. dominulus* to thrive in human-disturbed habitat and the potential harm to human health caused by high density wasp populations (via allergic reactions to wasp stings) may make this species an increasingly important subject in the field of urban ecology. This broad applicability, in combination with the ease of studying the behavior, ecology and genetics of *P. dominulus* under field, semi-natural, and lab conditions, makes the species an excellent model organism for invasion biology.

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Appendix

Sampling methods for genetic study

In Tuscany, 5 females were netted in flight during the summer of 2003, and an additional 18 females were collected from an overwintering aggregation in November 2003. Females of this population aggregate in large mixed-colony clusters (Dapporto *et al.* 2004), so multiple matrilines were likely to be represented. We checked that this was indeed the case by using the partitioning feature of the program KinGroup (Konovalov *et al.* 2004) to locate probable full-sister groups within the sample. The program found three such groups, from which we randomly selected one representative for further analyses. The resulting Tuscany sample included 17 individuals. In the Massachusetts population, females were collected from 18 cooperative nesting associations in June 2003. Genetic data from these foundresses were also used in a different study (Liebert & Starks 2006). Because sisters often nest cooperatively, we first randomly selected one female from each association to avoid biasing the sample toward genetically similar individuals. To increase the sample size, we then added five females whose genotypes revealed that they were not related to their co-foundresses. For the Michigan population, future foundresses ("gynes") were collected in late summer 2003 from 35 nests. One female per nest was included in the analysis. In northern California, females were netted in flight while foraging in an open field in June 2004. Finally, in southern California, all females were collected in May 2004 from one massive colony containing over 80 females (P. Nonacs pers. comm.). These females were sorted into putative sibling groups using KinGroup and then one female per group was chosen to include in the analysis. Samples were either frozen immediately at –80 °C or stored first in either 100% acetone or 70%–100% ethanol before freezing.

Genotyping protocols

Genomic DNA was isolated from two legs per wasp by grinding the frozen tissue with sterile mini-pestles (Strassmann *et al.* 1996), then incubating the samples in 250 μl of a 5% Chelex® solution

(Crozier *et al.* 1999, modified slightly from Walsh *et al.* 1991). We then amplified nine microsatellite loci per wasp using primers developed for this species by Henshaw (2000) and dye-labeled with IRD800 (Pdom1CAG, Pdom2AAG, Pdom25AAG, Pdom117AAG, Pdom121AAG, Pdom122AAT, Pdom127bAAT, Pdom139AAC, Pdom140TAG). Finally, alleles were visualized on 6.5% denaturing polyacrylamide gels using a LI-COR single channel 4200 NEN Global Edition IR^2 DNA Analyzer and scored with SAGA^{GT} 2.1 software.