A Surprising Level of Genetic Diversity in an Invasive Wasp: *Polistes dominulus* in the Northeastern United States

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ABSTRACT We examined the population genetic structure of an extremely successful invasive wasp, *Polistes dominulus*. Although successful biological invasions of social insects have been associated with genetic bottlenecks, our research uncovered an unexpected level of genetic diversity in the northeastern U.S. invasion population. Compared with a previously studied European sample, the northeastern U.S. invasion population shows no significant reduction in gene diversity and no trace of a genetic bottleneck in the putative "introduction population." We identified multiple private microsatellite alleles in both Massachusetts and New York, which strongly suggests that the northeastern U.S. *P. dominulus* population arose from at least two independent introductions. Although a genetic bottleneck may enhance invasion success for some social insects, genetic and geographical data on this successful invader suggest that this wasp may represent the converse. Our results support immediate identification of genetic diversity in an invasion population before the occurrence of secondary introductions as an essential part of managing and controlling invasive species.

KEY WORDS invasion biology, paper wasps, microsatellites

A GENETIC BOTTLENECK MAY expose certain characteristics of the genome, e.g., nonadditive genetic variance, to selection. As such, a genetic bottleneck has the potential to significantly change the genetic composition of an introduction population and thus alter its ability to survive in a novel environment (reviewed in Lee 2002). Indeed, postbottleneck genetic changes have been suggested as a factor leading to both behavioral changes in invasive species (Holway and Suarez 1999) and allopatric speciation between an invasive population and its source population (Lee 2002). Accordingly, it is becoming increasingly important to examine non-native species using an evolution-based animal behavior perspective (Holway and Suarez 1999, Lee 2002). Here we examine the genetic diversity in populations of an invasive wasp, *Polistes dominulus*, an animal often considered a model system for evolution-based animal behavior studies (Queller et al. 2000).

Native to Europe, the paper wasp *P. dominulus* has had great success in a short period of time in the United States. First identified in Massachusetts in the late 1970s (Eickwort 1978, Hathaway 1981), this invasive wasp's range has expanded across over two-thirds of the United States (Staines and Smith 1995, Judd and Carpenter 1996, Arduser and Stevens 1999, Landolt and Antonelli 1999). Recently, *P. dominulus* has been observed on the West Coast (Landolt and Antonelli 1999, Cervo et al. 2000), leading to speculation that the west coast population is either a new invasion or that the wasp has expanded its range across the entire country in an advancing wave front. Because of its relatively recent U.S. invasion, potential secondary invasions, rapid range expansion, and well-documented success, *P. dominulus* is ideal for studies of invasion biology. Indeed, the animal has successfully survived the introduction, colonization, and dispersal stages—trademark of a successful invader (Sakai et al. 2001).

Polistes dominulus exhibits many of the life history traits characteristic of successful invaders (reviewed in Sakai et al. 2001). Cervo et al. (2000) hypothesize that *P. dominulus'* invasion success may be because of (1) a more generalist diet and shorter brood developmental times than native *Polistes* wasps, (2) reduced predation because of aposematic coloration, (3) a propensity for nesting in sheltered areas, and (4) release from normal parasitism pressures. There is support for a number of these hypotheses. For example, evidence exists suggesting that *P. dominulus* preferentially nests in sheltered areas (Starks 2003b) and that the animal experiences low rates of parasitism in its introduced range relative to its native range (Pickett and Wenzel 2000, Hughes et al. 2003). In addition, a recent study found that *P. dominulus* has higher colony productivity than the native *P. fuscatus* and attributed this characteristic to an earlier production of workers, a higher survival rate of foundresses, and a greater foraging rate (see also Pickett and Wenzel 2000, Gamboa et al. 2002). Although the data were insufficient for statis-

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tical analysis, Gamboa et al. (2002) suggested that *P. dominulus* does not experience intra specific aggression. This observation on wild populations is somewhat at odds with those on captive populations: nest usurpation (Starks 2001), nest adoption (Starks 1998, 2001), and aggression between conspecifics (Starks et al. 1998, Pickett et al. 2000) has been observed in enclosure populations and in neutral arenas. Aggression between nest-founding wasps, however, is rare, and this observation is central to a current hypothesis for the successful invasion of some social insects (reviewed in Starks 2003a). It has been argued that decreased population genetic variability in social insects may lead to enhanced invasion success because high levels of genetic similarity among spatially separate nests may decrease intra specific competition (Holway et al. 1998, Tsutsui et al. 2000, 2003). Assuming that the animal behaves nepotistically in its native range, conspecific competition may be reduced in the invaded territory because of the invader's inability to distinguish kin from nonkin (Starks 2003a).

Because the high background relatedness hypothesis suggests that low population genetic diversity influences the success of some invasive species, determining the level of genetic bottleneck an invader experiences at introduction is vital. A newly established population is likely to be much less genetically diverse than the population from which it is derived (Barrett and Kohn 1991). Here we compare published European *P. dominulus* gene diversities (Henshaw 2000) with genetic data gathered from populations near the northeastern U.S. introduction (23 generations after reported introduction). Typically, a population bottleneck is only detectable for a few dozen generations after introduction and is characterized by a reduction in low frequency alleles but not necessarily a reduction in the observed heterozygosity (Luikart et al. 1998). Such analyses of genetic data will allow us to determine if the population stemmed from a single introduction in 1978 followed by secondary founder events or if it is more likely that the current U.S. population arose through multiple introductions, which can produce a highly genetically diverse population under certain conditions (Sakai et al. 2001).

Materials and Methods

Specimen Collection. Seventeen to 24 *P. dominulus* females were collected from four geographically distant subpopulations ($n = 79$ total) in August 2001 by P. T. S. Animals originated from two populations separated by ≈444 km: Massachusetts (Andover, 42°39′30″ N, 071°08′15″ W; Carlisle, 42°31′45″ N, 071°21′00″ W, 23 km apart) and New York (Genoa, 42°39′13″ N, 076°34′21″ W; Ithaca, 42°26′49″ N, 076°29′00″ W, 24 km apart). Collected females were from different nests and represent 79 individual colonies.

DNA Extraction, Amplification, and Visualization. All genetic analysis was conducted in the ISIRF genetics laboratory in Dana Hall at Tufts University. Total DNA was extracted from one to three legs per wasp using 250 μl of a 5% Chelex solution (Walsh et al. 1991) with slight modification (Crozier et al. 1999). DNA extractions were diluted 1:1 with distilled water. Polymerase chain reaction (PCR) was performed using primers published by Henshaw (2000) labeled with IRD800. PCR was carried out using an Applied BioSystems GeneAmp PCR System 2700 thermocycler in 15-μl reactions: 1× reaction buffer (Promega), 25 mM $MgCl_2$, 200 μM each dNTP, 300 nM each primer, and 0.75 U *Taq* polymerase (Promega). Microsatellite visualization was carried out on 6.5% denaturing polyacrylamide using a LI-COR single channel 4200 NEN Global Edition IR^2 DNA Analyzer and scored with $SAGA^{GT}$ 2.1 software.

Statistical Methods. Observed and expected heterozygosities were calculated as in Nei (1987). Allele frequencies and relatedness (overall, within-population, subpopulation, and pairwise) were estimated using the program RELATEDNESS 5.0.8 (Queller and Goodnight 1989, Goodnight and Queller 1999). Tests for linkage disequilibrium, i.e., deviations from Hardy-Weinberg equilibrium (HWE), were calculated using the program GENEPOP 3.3 (Raymond and Rousset 1995) through "Genepop on the web" (http://wbiomed.curtin.edu.au/genepop). A Mantel test to determine if there is a correlation between genetic and geographical distance, as would be expected for a population that had radiated from a single introduction, was also performed using the program GENEPOP 3.3. Pairwise F_{ST} estimates were calculated using the program FSTAT (Goudet 2001). The number of private alleles in each population and genetic structure within and between populations was quantified using hierarchical *F* statistics (Weir and Cockerham 1984) with the program GENETIC DATA ANALYSIS (Lewis and Zaykin 2001).

The two-phased model in the program BOTTLENECK (Cornuet and Luikart 1996, Piry et al. 1999) was used to test if there had been a previous smaller effective population size (as would be expected in a single recent introduction) by testing for a reduction in allele diversity but not observed heterozygosity. BOTTLENECK also identifies recently bottlenecked populations by assessing whether there has been a modeshift in allele frequency from low (normal conditions) to intermediate (recently bottlenecked) (Luikart et al. 1998).

Using the method described in Noor et al. (2000), the presence of a secondary founder event in the two New York subpopulations was tested using a one-tailed *t*-test on one minus the proportion of shared alleles (1 − Psa). This was used as an indicator of genetic distance, comparing the average differentiation between Carlisle, MA (as the putative "source") and each of the New York subpopulations to the differentiation between the two New York (putative "secondary") subpopulations. A significant result would suggest that the differentiation between the New York subpopulations is less than the average of their differences to the Carlisle, MA, population and therefore consistent with a secondary founder event.

Finally, using the most diverse locus, the effective minimum invasion population size (i.e., the number of outbred reproductive females) was estimated under the assumption that all invading females survived to reproduce, were singly mated to a genetically distinct male, and were heterozygous for appropriate loci (i.e., all females carried three private alleles).

Results

General Genetic Characteristics. One locus was monomorphic and therefore uninformative, leaving 12 polymorphic and informative loci for further analysis. A linkage-disequilibrium test for independence of loci showed that, for the two New York subpopulations, the markers, Pdom1 and Pdom25, and Pdom122 and Pdom140 were segregating nonindependently of one another. No linkage was detected between these loci in either of the Massachusetts subpopulations. To ensure that results were unbiased, analyses were conducted with both all loci and only one of each of the linked loci. Local tests for HWE showed that the majority of loci and populations did not deviate from HWE, with the exception of marker Pdom140 in the Carlisle and Andover subpopulations and Pdom7 in the Ithaca and Andover subpopulations, which showed homozygote excesses. However, these excesses were not supported by the other 10–11 loci for either subpopulation. These results raise the possibility of a low level of nonrandom mating, although the *F* statistics do not support this possibility (see below). In addition, the marker Pdom7 showed a slight heterozygote deficiency in the Carlisle subpopulation. The gene diversity of the introduced northeastern U.S. population was not found to be significantly different from that of the native *P. dominulus* population (Henshaw 2000) when observed heterozygosities (paired *t*-test; $t_{12} = 0.120$, $P = 0.91$) and expected heterozygosities ($t_{12} = 0.906$, $P = 0.38$; see Table 1) were compared. Subsamples of $n = 8$ individuals were taken from each subpopulation to account for any bias in sampling regimen between the European population (Henshaw 2000) and our more widely distributed U.S. population. None of the randomly sampled subpopulations were significantly different from that of the native *P. dominulus* population for observed heterozygosities (Genoa: $t_{12} = -1.43$, $P = 0.18$; Ithaca: $t_{12} = -1.19$, $P = 0.26$; Andover: $t_{12} = -1.02$, $P = 0.33$; Carlisle: $t_{12} = 0.93$, $P = 0.37$) and expected heterozygosities (Genoa: $t_{12} = 0.981$, $P = 0.35$; Ithaca $t_{12} = -1.06$, $P = 0.31$; Andover: $t_{12} = -0.884$, $P = 0.40$; Carlisle: $t_{12} = -1.29$, $P = 0.22$).

Over the 12 informative loci, private alleles were identified in each of the four subpopulations (Table 2). When the four subpopulations are grouped into their respective states (Massachusetts and New York), New York has nearly two-fold more private alleles as Massachusetts. This result raises the possibility that the Massachusetts and New York populations were initiated as a result of separate invasions and that the New York invasion was more genetically diverse.

Table 1. Observed (H_O) and expected (H_E) heterozygosities of *P. dominulus* wasps from one European and four Northeastern U.S. populations

Locus	European ($n = 8$)[a]	Northeastern United States ($n = 79$)
Pdom 1	$H_O = 0.38$ (3)	$H_O = 0.73$ (12)
	$H_E = 0.41$	$H_E = 0.73$
Pdom 2	$H_O = 0.75$ (4)	$H_O = 0.22$ (5)
	$H_E = 0.63$	$H_E = 0.20$
Pdom 7	$H_O = 0.75$ (5)	$H_O = 0.61$ (5)
	$H_E = 0.73$	$H_E = 0.75$
Pdom 20	$H_O = 0.88$ (4)	$H_O = 0.50$ (5)
	$H_E = 0.63$	$H_E = 0.58$
Pdom 25	$H_O = 0.50$ (3)	$H_O = 0.75$ (5)
	$H_E = 0.53$	$H_E = 0.78$
Pdom 93	$H_O = 0.63$ (2)	$H_O = 0.45$ (2)
	$H_E = 0.43$	$H_E = 0.50$
Pdom 117	$H_O = 1.00$ (9)	$H_O = 0.88$ (15)
	$H_E = 0.83$	$H_E = 0.88$
Pdom 121	$H_O = 0.63$ (6)	$H_O = 0.78$ (13)
	$H_E = 0.78$	$H_E = 0.87$
Pdom 122	$H_O = 1.00$ (9)	$H_O = 0.81$ (11)
	$H_E = 0.85$	$H_E = 0.79$
Pdom 127b	$H_O = 0.88$ (9)	$H_O = 0.78$ (14)
	$H_E = 0.80$	$H_E = 0.83$
Pdom 139	$H_O = 0.88$ (6)	$H_O = 0.45$ (7)
	$H_E = 0.72$	$H_E = 0.55$
Pdom 140	$H_O = 0.88$ (9)	$H_O = 0.64$ (10)
	$H_E = 0.85$	$H_E = 0.81$
Pdom 151	$H_O = 0.00$ (1)	$H_O = 0.00$ (1)[b]
	$H_E = 0.00$	$H_E = 0.00$
Average H	$H_O = 0.70$	$H_O = 0.63$
	$H_E = 0.63$	$H_E = 0.69$

n, number of individuals analyzed.
Number of alleles are listed in parentheses.
[a] Data from Table 1 of Henshaw 2000.
[b] Only 40 individuals analysed for this monomorphic marker.

Population and Subpopulation Level Genetic Characteristics. The overall estimate of Wright's (1965) $f = 0.044$ was not significantly different from zero ($-0.008 < 0.044 < 0.099$; 95% CIs, bootstrapping over loci 1,000 iterations), indicating no evidence for inbreeding. Estimates of differentiation across the entire sample, $F = 0.110$ ($0.068 < 0.110 < 0.154$); within each state, $\theta - S = 0.069$ ($0.050 < 0.069 < 0.088$); and within each subpopulation, θ-$P = 0.039$ ($0.016 < 0.039 < 0.061$) were low but significantly greater than zero, suggesting that there is genetic viscosity at both the total sample, population (i.e., state) and subpopulation (i.e., within-state) levels. Estimates of F_{ST} be-

Table 2. Number of private alleles, alleles common overall populations, and estimates of relatedness (SE calculated by jackknifing over loci) by subpopulation and state (New York and Massachusetts) over the 12 informative loci

Population	No. common alleles	No. private alleles	Relatedness
New York			
Genoa ($n = 17$)	65	4	0.0361 ± 0.0155
Ithaca ($n = 20$)	67	12	0.0111 ± 0.007
Total	63	27	0.0203 ± 0.0061
Massachusetts			
Andover ($n = 24$)	66	3	0.0182 ± 0.0107
Carlisle ($n = 18$)	61	5	0.032 ± 0.0096
Total	63	14	0.0268 ± 0.0097
Overall			0.0234 ± 0.0038

Table 3. Pairwise estimates of genetic differentiation between the four *P. dominulus* subpopulations

Subpopulation	Genoa	Ithaca	Andover	Carlisle
Genoa	—	0.300	0.376	0.471
Ithaca	**0.031 ± 0.010**	—	0.426	0.479
Andover	**0.074 ± 0.018**	**0.053 ± 0.014**	—	0.182
Carlisle	**0.092 ± 0.018**	**0.066 ± 0.019**	**0.032 ± 0.016**	—

Above the diagonal are pairwise 1-Psa estimates of gene diversity after Noor 2000. Below the diagonal are F_{ST} estimates ± SE, with those values significantly greater than zero (using 95% CIs) in boldface type.

tween each pair of subpopulations also revealed that all were genetically differentiated (Table 3). These results suggest within-state structure in both the New York and Massachusetts samples.

Relatedness estimates for both states and for each subpopulation were low but significantly greater than zero (Table 2). These relatedness estimates further support possible low-level substructuring within each of the states. In addition, each subpopulation contains individuals from multiple matrilines, and no single family was overrepresented in any of the samples.

Following the methods of Noor et al. (2000), we used the proportion of shared alleles to determine if the two New York subpopulations arose by the same introduction. Because this method is specifically designed for detection of secondary invasions, we used the Carlisle, MA, population as the putative source population for comparative purposes. The test for proportion of shared alleles between the two New York subpopulations was not significant ($P = 0.390$), indicating that the two New York subpopulations are genetically distinct and that it is very unlikely that they came from the putative MA source population.

Within Subpopulation Level Genetic Characteristics. A matrix was constructed where relatedness was estimated between all pairs of individuals, which revealed several biologically meaningful relationships. There were 17 pairs of individuals that showed relatedness not significantly different from 0.375 (0.382 ± 0.055), which would be the case if the two individuals were the offspring of full sisters (i.e., the individuals are cousins). Subpopulations Genoa, Ithaca, Andover, and Carlisle showed 24, 6, 21, and 19 cousin pairs, respectively (of a possible 135, 189, 275, and 152 pairs, respectively). These data suggest at least some degree of natal philopatry.

The test for detecting a mode shift in frequency distribution of alleles revealed none of the populations to be shifted; therefore, alleles at low frequencies were not the most abundant (as is usually the case for populations that have been through a recent bottleneck; Luikart et al. 1998). However, a standardized differences test using 85% stepwise mutation model and 15% infinite allele model revealed the Genoa subpopulation to be depauperate in allele numbers relative to gene diversity ($P = 0.026$). These results indicate that the Genoa population may be only recently established, but the remainder of our tested northeastern U.S. invasion population has not recently been through a genetic bottleneck.

Mantel Test for Genetic Isolation by Geographic Distance. The data were also examined for evidence of genetic isolation by geographical distance between all four subpopulations. The mean geographical distance between pairs of subpopulations was 30 km (smallest, 22 km; largest, 473 km). Mantel's tests were calculated with a rejection zone from 10,000 random permutations. Results of this exact test showed no correlation between genetic distance and geographic isolation ($P = 0.077$), which is consistent with multiple independent and genetically diverse introductions for both states.

Under the assumption that each state was colonized by a separate introduction, the minimum effective number of founding outbred females was calculated to be >3 and >4 outbred using the most polymorphic locus (Pdom117) for the Massachusetts and New York populations, respectively.

Discussion

Our genetic analysis uncovered a surprising level of genetic diversity in this invasive insect. Given the number of private alleles present in all four of our samples and because the animal was only identified in the United States 25 yr ago, it is unlikely that the level of allelic diversity observed in these four populations is caused by mutation alone. On the basis of these results, we were able to reject the hypothesis that high background relatedness is a significant contributing factor to the invasion success of *P. dominulus.* Our results from 12 highly polymorphic loci are also sufficient to reject the null hypotheses that there has been a single introduction of *P. dominulus* in the northeastern United States.

If the initial introduction population contained multiple females and spread to new sites as a function of normal dispersal patterns, we would expect (1) a decrease in genetic diversity with increasing distance from the point of introduction ("source population") and (2) very few private alleles in the more distant populations. Alternatively, if multiple independent invasions occurred, we would expect (1) no discernable pattern of genetic diversity with broad geographic location and (2) the presence of private alleles in those populations initiated through independent introductions. Our Carlisle population is closest to the reported site of introduction into the United States (Eickwort 1978, Hathaway 1981) and shows no sign of genetic bottleneck or significant levels of inbreeding.

Carlisle is also most likely not the source of the New York population because private alleles were identified in all four locations (Table 2), the 1 − Psa test showed no significant similarity within New York, and no discernable correlation between the level of genetic diversity and geographic location was observed.

Because it is unlikely that the New York population is the result of a secondary founder event from a Massachusetts source population or that the New York population is a result of a radiation from the Massachusetts population, our data best support the hypothesis that multiple independent *P. dominulus* invasions have occurred in the northeastern United States. However, we cannot exclude the idea that the Andover, MA, subpopulation may have been the result of radiation from the Carlisle subpopulation, as suggested by a lower level of pairwise gene diversity than observed between other pairs of subpopulations (Table 3, above diagonal) and low but significant pairwise F_{ST} estimate (Table 3, below diagonal).

Future investigations may benefit by examining the relationship between genetic diversity and time (i.e., a longitudinal study) and the relationship between geographic location and mitochondrial haplotypes, and determining the genetic structure of populations across the United States. It is imperative that the genetic diversity of the other major populations of *P. dominulus* in the United States be analyzed in the near future. In addition, genetic comparison to the native European population would assist in determining if the genetic structure in the introduced *P. dominulus* population has changed significantly, possibly in response to selection in a novel environment (Lee 2002).

The fact that we only had gene diversity from a small native European population (Henshaw 2000) as a comparison with introduced U.S. gene diversities was not ideal. However, because our data show no sign of an initial founder event in Massachusetts, the diversity within the U.S. population stands alone as an indicator of the population genetic status of this invader. In addition, we randomly subsampled eight individuals from each of our four subpopulations, and none showed significant differences from Henshaw's European sample for either the observed or expected heterozygosities. In future work, it will be important to compare more than just gene diversity from the European population in the hope of localizing the region/s from which the U.S. introductions came.

From a behavioral ecologist's perspective, *P. dominulus* may be the best-studied social wasp (Queller et al. 2000). Because behavior is becoming an increasingly important tool for population ecologists, *P. dominulus* may also prove to be an ideal study animal for questions of invasion biology (Starks 2003a). Because of (1) its recent U.S. invasion, (2) the potential secondary invasions, (3) its rapid range expansion, and (4) the previous work on the genetics (Henshaw 2000) and behavior of the wasp (e.g., Reeve 1991, Turillazzi and WestEberhard 1996), *P. dominulus* is ideally suited to act as a model system to test processes of invasion success in social insects. We believe our results serve as a complement to the current studies of invasion success in social insects, such as the severely bottlenecked argentine ant (e.g., Tsutsui et al. 2000) and the introduced African honey bee, which shows initial hybridization with European honey bees but retains a majority of African characteristics (reviewed in Schneider et al. 2004).

In closing, our data suggest that the northeastern U.S. *P. dominulus* invasion population was initiated by multiple independent introductions. The presence of such high genetic diversity in an invasion population was unexpected and may prove useful to behavioral ecologists examining kin selection theory in these populations and conservation geneticists for management of invasive species. Historically, some of the most successful invaders have been the result of multiple introductions, often producing an introduced population that is more genetically diverse than in a highly structured native population (reviewed in Sakai et al. 2001). Therefore, there is strong evidence to support timely analysis of the genetic structure of an invasive population before subsequent invasions allows a species to establish. Although a genetic bottleneck may enhance invasion success for some social insects, our data on this extremely successful invader clearly suggest that a severe genetic bottleneck was not necessary for the establishment and expansion of *P. dominulus.*

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