

Sexual interactions and nestmate recognition in invasive populations of *Polistes dominulus* wasps

A. E. Liebert · N. Wilson-Rich · C. E. Johnson ·
P. T. Starks

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Abstract Many social insect species have mating systems or recognition abilities that minimize the chance of inbreeding. In haplodiploid systems, inbreeding is especially costly due to the production of sterile offspring such as diploid males. Diploid males (and their triploid offspring) have been identified in invasive populations of the paper wasp, *Polistes dominulus*, but to date have not been reported in its native populations. Due to the degree of genetic diversity in the invasive populations, it is unlikely that the production of these genetic ‘misfits’ is the result of a genetic bottleneck alone, but rather that errors in nestmate recognition may play a role. Here, we investigated sexual interactions and nestmate recognition in male and female *P. dominulus*. We observed nine types of behavioral interactions (55 h of behavioral observation consisting of 1,514 interactions) from triads of paper wasps composed of one gyne (female) and two males—one nestmate male and one non-nestmate male. The frequency of male- or female-initiated aggressive behavior did not differ between nestmates or non-nestmates. Non-nestmates were more likely to attempt to copulate with the gyne, but successful copu-

lations were very rare and occurred between non-nestmates and nestmates. We discuss these results within the context of invasion biology.

Keywords Sexual selection · Competition · Hymenoptera · Paper wasps · Diploid males

Introduction

Invasive organisms pose major economic and ecological concerns for conservation biologists (Lockwood et al., 2007). A biological invasion is the geographical expansion of a species into an area it has not previously occupied (Ehler, 1998). The invasion process may involve multiple introductions of small populations that can survive rapid habitat transitions (Lee, 2002). These small populations likely reproduce via inbreeding, which can pose strong constraints on fitness by allowing for the expression of deleterious recessive alleles and decreasing allelic diversity within the gene pool (Fonseca et al., 2000; Tsutsui et al., 2000; Zeisset and Beebe, 2003; Rasner et al., 2004).

Eusocial Hymenoptera are especially successful invasive species because of their reproductive and dispersal strategies (Moller, 1996). Isolated females can colonize without a mate because they are able to store sperm; the haplodiploid genetic system also allows uninseminated females to produce haploid offspring (Moller, 1996). However, small colonizing populations of certain species may face difficulties due to the production of genetic ‘misfits’ known as diploid males. Diploid males are produced because of the Hymenopteran complementary sex determination (CSD) mechanism, which requires heterozygosity at one or more sex-determining loci to produce normal diploid females (Fig. 1; Whiting, 1924; Crozier,

A. E. Liebert (✉)
Department of Biology, Framingham State College,
100 State Street, Framingham, MA 01701-9101, USA
e-mail: aliebert@framingham.edu

N. Wilson-Rich · C. E. Johnson · P. T. Starks
Department of Biology, Dana Laboratories,
Tufts University, Medford, MA 02155, USA

N. Wilson-Rich
e-mail: noahwilsonrich@gmail.com

C. E. Johnson
e-mail: caitlinejohnson@gmail.com

P. T. Starks
e-mail: philip.starks@tufts.edu

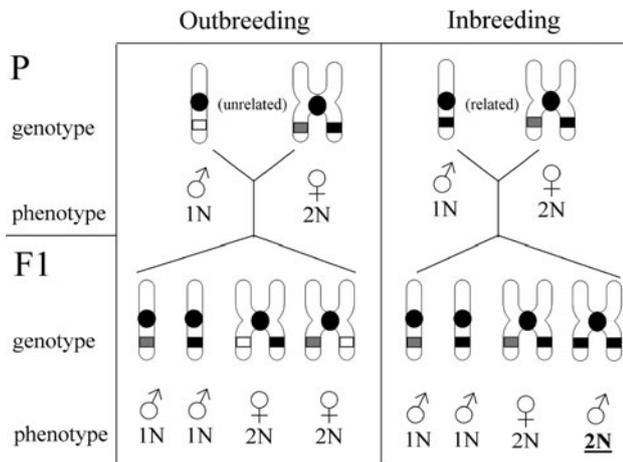


Fig. 1 Single-locus complementary sex determination. In haplodiploid species such as *P. dominulus*, males are typically haploid (1N) and females are typically diploid (2N). Under single-locus CSD, sex is determined by a single locus with multiple alleles in a population (above: white, gray, and black). Heterozygosity results in a female phenotype and hemi- or homozygosity produces a male phenotype. Brother–sister inbreeding results in the production of diploid males (bottom right), which do not contribute to colony productivity and are functionally sterile

1971; van Wilgenburg et al., 2006). Homozygosity at the sex-determining locus or loci results in diploid males (Whiting, 1933, 1943). Such individuals would normally be female because they are diploid, but instead develop into males.

Diploid males pose fitness costs to the colony because they consume resources but do not contribute to colony productivity, and are functionally sterile (see Liebert et al., 2004). Indeed, some species such as the honey bee *Apis mellifera* cannibalize larvae in worker cells that develop a male phenotype (Woyke, 1963). However, the expected proportion of diploid males produced in the worker brood of species with CSD is only ~50% if controlled by a single locus, and would be even lower for multiple-locus CSD. Because of this, females that fertilize their eggs with sperm from related males would still produce at least 50% female workers. If unrelated males are rare, inbreeding among colonizing individuals could therefore lead to higher fitness than the alternative of not mating at all, since unmated females that successfully produce offspring would produce only haploid males and no female workers.

Polistes dominulus is a native paper wasp of Eurasia and Northern Africa, which has recently become a highly successful invasive species in Australia, South America, and North America (reviewed in Liebert et al., 2006). The existence of diploid males in North American paper wasps was first suggested by Liebert and colleagues (2004) when they documented the presence of triploid females, and then confirmed soon after in multiple populations in Massachusetts (Liebert et al., 2005) as well as a single population

in California (Liebert et al., 2008). Even though diploid males have no putative role in colony fitness, their presence might be indicative of a process that sustains invasive populations in the short term. Females in a small colonizing population may at first have limited or no access to unrelated males. As mentioned above, the fitness costs of not mating may be greater than producing a reduced worker brood. Hence, if the production of diploid males is limited, then an invasive population of *P. dominulus* may be able to sustain the inbreeding depression within a small population until more alleles enter the gene pool upon subsequent invasion events. Indeed, data support multiple invasion events in the North American population of *P. dominulus* (Johnson and Starks, 2004; Liebert et al., 2006).

Given the fitness costs associated with inbreeding, however, natural selection should favor mating behaviors that reduce its occurrence. Reeve's (1989) conspecific acceptance threshold model provides a theoretical framework to understand the context dependence of nestmate recognition and inbreeding avoidance (see Starks et al., 1998a, 1998b). In this model, an individual evaluator (Liebert and Starks, 2004) compares the cues of a potential mate with an internal template, and either accepts or rejects that mate based on the position of the “acceptance threshold”. This threshold is determined by balancing the relative costs of mating with a relative (“acceptance error”) versus not mating with a nonrelative (“rejection error”), given the probability of encountering related and unrelated mates. Nestmate recognition in *Polistes* has been widely studied and these wasps are known to possess colony-specific chemical signatures determined by a unique combination of cuticular hydrocarbons also present in the nest paper (reviewed in Gamboa, 2004). We also know that male *Polistes* wasps appear to possess nestmate recognition abilities (Shellman-Reeve and Gamboa, 1985; Ryan and Gamboa, 1986), and that *P. dominulus* females can discriminate nestmates from non-nestmates (Starks et al., 1998a). Hence for *P. dominulus*, inbreeding avoidance could be accomplished either through a mating system that minimizes the probability of encountering relatives or via nestmate recognition and subsequent rejection of related mates.

P. dominulus in its native range has a lek-based mating system in which large numbers of males gather at landmarks and either aggressively defend small territories (residents) or patrol a wider area (transients) (Beani and Turillazzi, 1988). Because females visit these locations to find mates, inbreeding is not likely in a large natural population. Indeed, studies of *P. dominulus* in Italy found that males attempting copulations did not discriminate between nestmates and non-nestmate females (Beani and Turillazzi, 1988). It is, therefore, likely that native *P. dominulus* males have a tolerant acceptance threshold, which would

minimize the risk of rejection errors. Studies of the mating system of *P. dominulus* in the introduced range are lacking, but if the mating system is comparable to reports from the native range, such a tolerant threshold could result in higher rates of inbreeding due to small population size or difficulty of finding mates. However, this does not address female choice, which may be more relevant for *Polistes* mating; female *P. fuscatus* appear to maintain some control over mate choice by successfully rejecting male attempts at copulation (Post and Jeanne, 1983), and perhaps by a post-copulatory mechanism of selective sperm utilization. Although this has not been studied directly, genetic studies of *P. dominulus* indicate an effective mate number of one (Strassmann, 2001) despite observations of multiple copulations (Beani and Turillazzi, 1988). The presence of diploid males in invasive populations suggests that mating among nestmates does occur. However, no behavioral studies exist that directly examine whether *P. dominulus* wasps from the introduced range exhibit nestmate discrimination in a mating context. In this study, we begin to address this question by investigating whether male and female *P. dominulus* wasps from an invasive population known to produce diploid males discriminate between nestmates and non-nestmates. Specifically, we examine the agonistic behavioral interactions, copulations, antennations, and chases within triads of wasps including a gyne, a nestmate male, and a non-nestmate male.

Methods

Over a 2-year period, we collected 25 *P. dominulus* nests from three field sites in Massachusetts, USA (North Grafton, Stow, and Medford). We transported all nests to the International Social Insect Research Facility (ISIRF) housed at Tufts University in Medford ($N = 16$ nests in September 2004, $N = 9$ in July 2005). We reared all nests in the ISIRF live animal facility at approximately 22°C on a 12-h photoperiod. We housed each wasp nest with respective wasps in a box (26 cm × 24 cm × 62.5 cm) constructed with untreated wooden frames and mesh screening on one side (26 cm × 62.5 cm). We fed wasps on a diet of *Galleria mellonella* wax worms and a 25% honey water solution ad libitum. Gynes and males were separated at least 1 week prior to triad trials, whereby gynes remained in the nest box with their natal nest, and we isolated males in plastic storage containers by colony. Whenever possible we used females that we observed eclosing in the lab to ensure that they were uniseminated gynes. Field-collected females from nests collected in September 2004 were determined to be gynes based on low wing wear to distinguish them from workers.

Although it is possible that some of these females were already inseminated, it is not known whether females return to their natal nest after mating in these populations. All wasps used in the study were exposed to their natal nests for at least 1 day to ensure learning of nestmate recognition cues, which has been shown to occur within about 4 h after eclosion (Pfennig et al., 1983.)

Triads consisted of one gyne, one nestmate male and one non-nestmate male matched for body weight. Observations occurred between 19–26 September 2004 and 22–27 September 2005. We weighed and color marked each wasp (Testor's enamel paint) and placed triads of wasps in clear plastic trapezoidal observation arenas (base: 21.5 cm × 13.5 cm, top: 19.5 cm × 12 cm, height: 13 cm), which proved ample space for behavioral interactions without forcing an interaction by proximity. Observers, blind to the nest origin of each wasp, recorded the frequency of nine different behavioral interactions (Table 1) after protocol reported in Pfennig et al. (1983). All observations took place indoors between 1000 and 1800 hours at room temperature, with a lamp placed above the arenas to simulate daytime sunlight. After 1 h of observation, we returned all wasps to their storage containers. We rinsed observational arenas with 70% ethanol between trials so as to minimize confounding effects of chemical residues that potentially could influence wasp behavior. No wasp was observed more than once.

Interactions between females and males were grouped into two categories (Table 1): agonistic (darts, lunges, bites, grapples, falling fights) and copulatory (attempted and successful copulations). Two other behaviors (antennations and chases) did not necessarily fit into one of these two categories. Antennating may be a recognition process involving the exchange of signals, which can result in either aggressive behavior or mating behavior. Male chasing of a gyne may indicate pursuit of a mate as opposed to aggression. Using Wilcoxon signed-rank tests, we compared the mean frequency of each general behavior, between the following pairs: gynes and male nestmates, gynes and male non-nestmates, and male nestmates and males non-nestmates. We used DataDesk 6.0 for the Mac for all statistical analyses.

Results

We observed 56 triads of wasps from 25 *P. dominulus* colonies for a total of 56 h and recorded 1,514 total interactions, 211 of which specifically involved copulatory behavior. The total counts as well as number of individuals performing each observed behavior are listed in Table 1.

Table 1 We observed and recorded the frequency of these nine behavioral acts to determine the context of nestmate discrimination and mate choice in *P. domimulus*

Behavioral category	Behavior	Description	Total number of observations (number of individuals)					
			NM → G	G → NM	NNM → G	G → NNM	NM → NNM	NNM → NM
Agonistic	Dart ^a	Rapid movement toward a conspecific	10 (3)	6 (6)	6 (3)	11 (5)	6 (4)	8 (4)
	Lunge	Dart with contact	12 (6)	16 (9)	38 (10)	29 (12)	23 (8)	54 (11)
	Bite	Mandible-to-body contact	8 (1)	17 (11)	4 (2)	43 (11)	22 (6)	25 (11)
	Grapple	Wrestling	0	0	0	0	12 (6)	39 (7)
	Falling fight	Escalated grapples until both individuals fall	0	0	0	0	3 (2)	6 (2)
Copulatory	Attempted copulation	Male climbing female dorsum, curling tip of abdomen downward toward female genitalia, but no genital linkage	60 (13)		123 (19)			
	Successful copulation	Same as attempted copulation, but genital linkage achieved	3 males		8 males			
Other	Antennation	Antenna-to-antenna or antenna-to-body contact	118 (37)	105 (32)	114 (35)	137 (35)	23 (11)	34 (11)
	Chase	Pursuit of a conspecific	35 (20)	0	70 (21)	0	0	0

Descriptions of behavior were from Larch and Gamboa (1981), Pfennig et al. (1983), Reeve (1991), and Starks et al. (1998a). The last six columns show the total counts for each observed behavior, as well as the number of individuals observed to initiate the behavior for each pair within the triad

G gyne, NM nestmate male, NNM non-nestmate male

^a Darts are listed as agonistic in accordance with traditional categorization, although they may rather serve a communicative role (see Sumana and Starks, 2004)

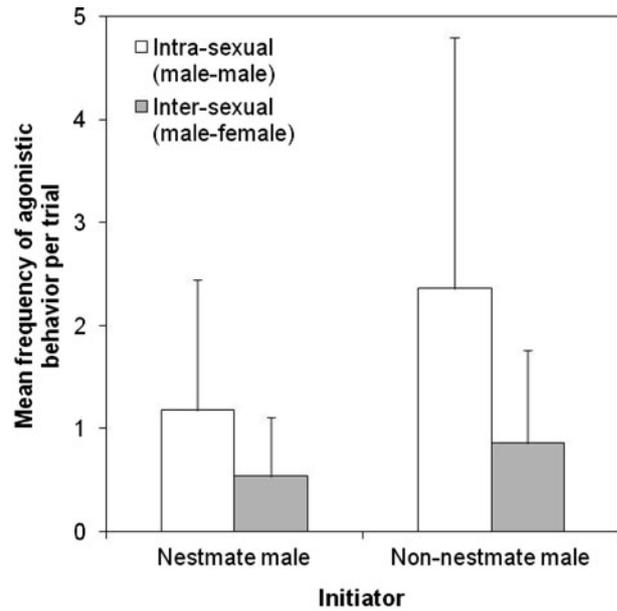


Fig. 2 Intra- and inter-sexual agonistic behavior initiated by *P. domimulus* males. Agonistic behaviors included darts, lunges, bites, grapples, and falling fights. Columns represent mean (\pm SE). Data represent the mean frequency of all agonistic behaviors per trial as initiated by males with respect to relatedness to gyne

Agonistic interactions

Intra-sexual (male–male) aggression was initiated slightly more often by non-nestmates of the gynes than by nestmate males, but this difference was not statistically significant (Wilcoxon signed-rank test, $z = -1.42$, $p = 0.16$; Fig. 2). Inter-sexual (male–female) agonistic behavior did not differ between nestmates and non-nestmates, in terms of male aggression toward the gyne (Wilcoxon signed-rank test, $z = 0.95$, $p = 0.343$; Fig. 2), or aggression initiated by the gyne toward the males ($z = -0.99$, $p = 0.321$).

Copulation behavior

Non-nestmate males attempted to copulate with gynes significantly more often than did nestmate males (Wilcoxon signed-rank test, $z = -2.57$, $p = 0.01$; Fig. 3). Most attempts did not result in successful copulations; only 11 out of 32 males that attempted copulations were successful overall, including 8 non-nestmates and 3 nestmates (Fig. 4). These proportions did not differ from the null expectation of equal copulation rates for nestmates and non-nestmates (sign test, $p = 0.23$). However, the likelihood that a non-nestmate male successfully copulated differed significantly from zero (one-sample sign test, $p < 0.01$), whereas the likelihood that a nestmate male successfully copulated did not differ significantly from zero (one-sample sign test, $p = 0.25$). One of the three nestmate males and three of the

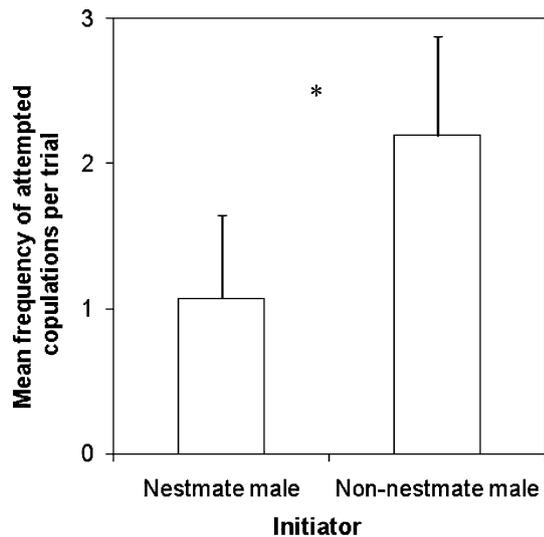


Fig. 3 Non-nestmate males attempted to copulate with gynes significantly more often than did nestmate males (Wilcoxon signed-rank test, $z = -2.57$, $p = 0.01$). Columns represent mean (\pm SE). Data represent the mean frequency of each behavior per trial as initiated by males with respect to relatedness to the gyne

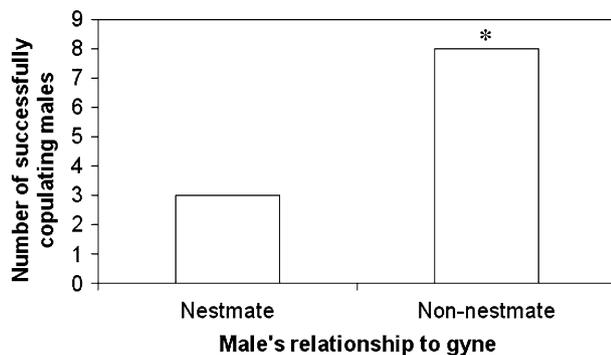


Fig. 4 Number of *P. dominulus* males that successfully copulated with the gyne. Eight non-nestmate males successfully copulated, while only three related males did so. These proportions do not differ from a null expectation of equal likelihood of copulating with nestmates and non-nestmates (sign test, $p = 0.23$) However, the likelihood that a non-nestmate male successfully copulated differed significantly from zero (one-sample sign test, $p < 0.01$), whereas the likelihood that a nestmate male successfully copulated did not differ significantly from zero (one-sample sign test, $p = 0.25$)

eight non-nestmate males successfully copulated with the female more than once. In two trials, the female copulated with both the nestmate male and non-nestmate male.

Other interactions

Antennations occurred between all three individuals at similar frequencies, with no observed preferences between any groups of two. Females did not antennate more with either the nestmate male or the non-nestmate male

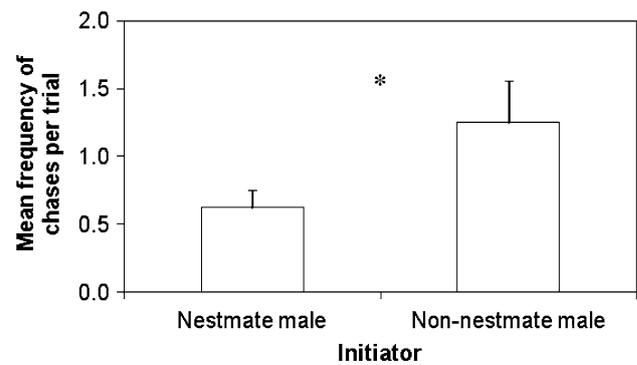


Fig. 5 Chases directed toward the gyne were initiated by the non-nestmate male significantly more than by the nestmate male (Wilcoxon signed-rank test, $z = -2.18$, $p = 0.03$). Columns represent mean (\pm SE). Data represent chase behavior per trial as initiated by males with respect to relatedness to gyne

(Wilcoxon signed-rank test, $z = -1.24$, $p > 0.1$). Chases directed toward the gyne were initiated by the non-nestmate male more so than by the nestmate male (Wilcoxon signed-rank test, $z = -2.18$, $p = 0.03$; Fig. 5).

Discussion

Our results demonstrate that *P. dominulus* males are able to discriminate whether a female is a nestmate or non-nestmate in their pursuit of a mate. Males were significantly more likely to chase and attempt to copulate with a non-nestmate gyne than a nestmate. However, successful copulations were rare and occurred between both nestmates and non-nestmates. These results differ from previous findings by Beani and Turillazzi (1988) that male *P. dominulus* in a native population do not discriminate relatives and nonrelatives in attempted copulations. One possible reason for this difference is that the Beani and Turillazzi (1988) study was conducted in a larger cage with multiple males and females. It is, therefore, possible that all *P. dominulus* males are capable of nestmate recognition in a mating context, but do not discriminate nestmate when in the more natural situation of numerous females visiting the lek. Alternatively, invasive populations of *P. dominulus* may demonstrate more strict thresholds of nestmate discrimination in the mating context. Further study is needed to distinguish between these two possibilities.

Overall, the rate of successful copulations was low. This may have been due to the lack of stimuli for a natural mating context; however, this finding is consistent with the well-documented rarity of observing mating behavior of *Polistes* wasps even in long-term studies (Beani, 1996), and provides further evidence that females may be maintaining control over mate choice by avoiding copulation. Our data suggest that females may selectively accept copulation attempts by

non-nestmate males at a higher rate than nestmates. These results are consistent with results in the sympatric native congener, *P. fuscatus*, which show that female *P. fuscatus* prefer to mate with non-nestmates (Ryan and Gamboa, 1986). However, it is unclear why females reject a high proportion of copulation attempts, and also why some of the accepted copulations were from nestmate males.

As previously mentioned, *P. dominulus* has diploid males and triploid females in the invasive population (Liebert et al., 2004, 2005) but to date none have been reported from the native region. Liebert et al. (2006) did not find triploid females in samples tested from the native range that were comparable to sample sizes from invasive populations where triploids were found. Cotoneschi and co-workers (2007) collected late instar *P. dominulus* larvae from eight pre-emergence colonies near Florence, Italy and found an absence of males. Diploid males are most commonly found during the pre-emergence period in spring and should have been found during this time if they had occurred in the population (Pardi, 1942; as cited in Cotoneschi et al., 2007). Cotoneschi and co-workers then performed genetic analysis on four microsatellite loci across 70 *P. dominulus* larvae collected from the same area 2 months later and found no triploid females. Had triploid females existed in this native population, they likely would have been found during this time later in the season (see Liebert et al., 2004).

The production of diploid males and triploid females observed in invasive *Polistes* populations (Liebert et al., 2004, 2005) could theoretically be the result of inbreeding or of low allelic diversity at the sex-determining locus, or both, in a very small population where mate choices are limited to related individuals. Although it is possible that a genetic bottleneck has occurred at the sex-determining locus, microsatellite data reveal relatively high genetic diversity in the studied invasive populations (Johnson and Starks, 2004; Liebert et al., 2006). Our observations of three incidents of copulation between nestmates (putative brother–sister inbreeding) suggest that inbreeding is a possible cause of diploid male production. But this apparently costly behavior could actually benefit invasive populations by stabilizing the population in the early stage of colonization (Fig. 2). It would be fortuitous if both male and female *P. dominulus* wasps have relatively tolerant acceptance thresholds for discriminating relatedness of potential mates, due to the low probability of encountering relatives in the lek mating system in native populations. Even if this threshold shifted to become more strict if the encounter rate with related males was to increase in a newly colonized population, some percentage of acceptance errors, in which a female failed to reject a nestmate male, would still be expected (Reeve, 1989). These “errors” could increase the chances of success of the colonizing population by ensuring that mating would take place even with a high probability of inbreeding.

Since their first discovery in North America by Eickwort (1978; Hathaway, 1981), invasive populations of *P. dominulus* are now found continent-wide (Liebert et al., 2006). Recent genetic analysis of a hypergynous cooperative nesting association of *P. dominulus* from Los Angeles, CA suggests that the frequency of genetic misfits may be decreasing over time (Liebert et al., 2008). This massive 613-cell nest contained 84 adults, only one of which was a genetic misfit—a diploid male. Additional microsatellite analyses showed that the allelic richness within the southern California *P. dominulus* population had in fact increased from 2001 (Liebert et al., 2006) to 2004 (Liebert et al., 2008). The presence of only one diploid male may indicate the relative ease of finding unrelated males in the southern California *P. dominulus* population (Liebert et al., 2008).

Our results show that males from an invasive population of *P. dominulus* are capable of nestmate recognition in a sexual context. In native populations, nestmate recognition at natural leks is probably not of great importance due to the low probability of encountering relatives in these large aggregations. However, this ability may play an important role in small invasive populations. Comparative studies examining acceptance thresholds for mating with relatives across native and invasive populations would help illuminate whether colonizing populations do indeed shift their acceptance thresholds in a new environment. The extent of female choice by *Polistes* females also remains unexplored. Our results confirming that female *P. dominulus* copulate with multiple males, despite evidence indicating an effective mate number of one (Strassmann, 2001), suggests the existence of some type of post-copulatory female choice. However, why there is such a low rate of copulation, despite multiple attempts by the males, remains an unanswered question.

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