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**Permalink**
https://escholarship.org/uc/item/7hs1422h

**Journal**
Journal of Insect Behavior, 21(2)

**ISSN**
0892-7553

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**Publication Date**
2008-03-01

**DOI**
10.1007/s10905-007-9108-x

Peer reviewed

# Extreme Polygyny: Multi-seasonal "Hypergynous" Nesting in the Introduced Paper Wasp *Polistes dominulus*

**Aviva E. Liebert · Julia Hui · Peter Nonacs · Philip T. Starks**

**Abstract**  In temperate climates, female paper wasps typically initiate new colonies in the spring. Several nest-founding tactics have been documented in *Polistes* species, including solitary nest initiation, joining a cooperative association, usurping an existing nest, or adopting an abandoned nest. Occasionally, exceptionally large groups of females have also been found reusing nests from the previous season. Here we report this phenomenon in introduced populations of the Eurasian species *Polistes dominulus*. We describe in detail the demographic and genetic characteristics of one such spring colony from Los Angeles, California, USA, which was collected with 84 associated adults and all stages of developing brood in its 613 cells. Genetic and morphological data indicate the presence of multiple reproductively active females of varying relatedness, as well as many nonbreeding females, including probable early-produced offspring. Despite some evidence of chaotic social conditions, the colony appeared to have been highly productive. Additional observations of similar colonies are needed to determine how control is maintained within such a large breeding aggregation.

**Keywords**  Pleometrosis · foundress association · invasive species · diploid males · hymenoptera

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## Introduction

*Polistes* paper wasps are a model genus for studies of social evolution, due in part to their flexibility in colony initiation behavior (West-Eberhard 2006). Nest-founding *Polistes* females (foundresses) may exhibit one of several tactics, including solitary nest initiation, joining a cooperative association, usurping an existing nest, or adopting an abandoned nest (Reeve 1991; Nonacs and Reeve 1993; Starks 1998). Foundresses typically build new nests rather than reuse old combs, though nest reuse has been reported in a few species: *Polistes annularis* (Strassmann 1983); *Polistes humilis*: (Cumber 1951; Itô 1986); and some European populations of *Polistes dominulus*: Giovanetti et al. 1996, as cited in Cervo et al. 2000). Occasional nest reuse by particularly large foundress groups has also been reported (*P. annularis*, 21 and 28 females, Strassmann 1983; *P. humilis*: 16–36 females, Itô 1986).

In this paper we report a similar phenomenon in introduced populations of *P. dominulus*. On these multi-seasonal, "hypergynous" colonies, an unusually large group of females reuses and expands a nest from a previous season, thus producing a massive colony in the spring when new temperate zone colonies are typically initiated. A small number (3–4) of hypergynous *P. dominulus* nests were observed in June 1993 in Ithaca, New York (P. Nonacs, pers. obs.) 2 years after the species was first reported in this state (Jacobson 1991) and 15 years after the first North American observation of *P. dominulus* in Cambridge, Massachusetts (Eickwort 1978). Two hypergynous colonies were also observed in 2004 and 2005 in a nascent population in Los Angeles, CA, USA where *P. dominulus* was first seen in 2001 (P. Nonacs, pers. obs.). Here we examine one of these Los Angeles nests in detail.

Of particular interest to our study was the kin structure and breeding status of females in such an unusually large group. The average size of mature *P. dominulus* colonies is 149 cells (Turillazzi 1980) ranging as high as 477 cells in one specimen from Italy (Guiglia 1972). In most *P. dominulus* populations, 40–70% of colonies are singly founded (Queller et al. 2000; Tibbetts and Reeve 2003; Liebert and Starks 2006). Foundress group sizes typically range from one to ten and average between two and five females (Queller et al. 2000; Tibbetts and Reeve 2003; Cant et al. 2006; Liebert and Starks 2006), although groups as large as 19 have been reported from one population in southern Spain (Shreeves et al. 2003; Cant and English 2006); occasional large groups of over 30 individuals have also been observed on reused nests in this Spanish population (J. Field, pers. comm.).

A large body of *Polistes* research has focused on the benefits of cooperative nesting associations. Multiple foundress colonies generally have higher survivorship than solitary nests (reviewed in Reeve 1991), and many studies have found a positive linear relationship between colony productivity and group size (Cant and Field 2001; Shreeves et al. 2003; Liebert and Starks 2006). However, *Polistes* foundress associations tend to form a linear dominance hierarchy (Reeve 1991), and *P. dominulus* studies have found that typically one female monopolizes reproduction (Queller et al. 2000; Liebert and Starks 2006; Nonacs et al. 2006). Non-reproducing subordinates in such groups are thought to reap either indirect benefits by joining relatives, or direct benefits via eventual inheritance of the dominant breeding position (Queller et al. 2000; Cant and Field 2001; Cant et al. 2006). Because an

inheritance queue on a hypergynous colony would presumably be too long for most females to have a reasonable chance of becoming dominant, we might expect a hypergynous association to consist of uniformly close relatives. This is apparently the case for *P. annularis* (Strassmann 1983) in which large foundress groups on new and reused nests were found to be comprised of former nestmates.

Alternatively, the association might lack a strict dominance hierarchy. Indeed, the ability of one dominant female to maintain reproductive control seems unlikely on such a large colony (Oster and Wilson 1978). Unlike some eusocial taxa, such as naked mole rats, in which dominant females suppress fertility of subordinates via pheromonal control (Faulkes and Bennett 2001), *Polistes* foundresses have been shown to maintain control behaviorally, either via direct aggression or differential oophagy (reviewed in Spradbery 1991). Even on a small colony, a *P. dominulus* foundress apparently is not able to physically prevent subordinates from laying eggs in empty cells, although she can later replace these with her own eggs (Liebig et al. 2005). To address these issues, we investigated the relatedness and breeding structure of the hypergynous association.

## Methods

### Colony Collection

The colony was collected from an eave of a house in west Los Angeles on May 6th, 2004. Collection took place early in the morning when temperatures were cool and all associated adults were likely to be present. Adult wasps were immediately placed into 100% acetone for DNA preservation (Fukatsu 1999) and the brood-filled nest was frozen at -80°C before shipping on dry ice to Tufts University, Medford, MA, USA. In a 4°C cold room, we removed brood from the nest and created a map on which we recorded the stage of the brood in each cell (egg, larval (L) instars L1, L2, L3, L4, or pupa). It was difficult to differentiate the fourth from the fifth larval instar, so we merged these into the L4 category. Adults were air-dried and their sex identified by morphology. All adults and brood were placed in individual tubes and frozen at -80°C until further analysis.

### Microsatellite Genotyping

We extracted DNA from all 84 adults and a sample of 96 (17.3%) of the brood. We selected the brood sample by first preferentially genotyping 18 pairs of tandem brood (more than one egg, larva, or pupa per cell), which we believed could shed light on the possible loss of reproductive control within the colony. Then we divided the nest map into four quadrants and chose a representative sample of brood from each. DNA was isolated from leg tissue of adults and pupae, head capsules or thorax tissue of larvae and pre-pupae, and entire eggs, and then amplified at seven microsatellite loci using primers developed for *P. dominulus* (Pdom1CAG, Pdom25AAG, Pdom117AAG, Pdom121AAG, Pdom122AAT, Pdom127bAAT, and Pdom140TAG; Henshaw 2000). Genotyping protocols were the same as in Johnson and Starks (2004), with some modification from Strassmann et al. (1996) for brood DNA extraction.

## Genetic Data Analysis

Our main goals in analyzing the genetic data were to determine (1) the kin structure of resident adults, and (2) the number of actively breeding females in the colony. We also used genotypic information to identify the sex of eggs and larvae. Because wasps are haplodiploid, males have one allele per locus while females have two. We therefore assumed that brood were haploid males if only one allele was visible at all seven loci. Although some of these individuals may have been diploids that happened to be homozygous at all loci, the probability of this occurrence is extremely low for any single wasp (using allele frequencies from the current sample of collected adults, $P=0.00057$).

To examine kin structure among adult females, we used the program Relatedness 5.0.8 (Goodnight and Queller 1999) to calculate pairwise and overall genetic relatedness. Population allele frequencies were calculated using ten individuals from this population that were collected while foraging. We also used the program KinGroup 1.0 (Konovalov et al. 2004), which uses a maximum-likelihood method to partition a set of genotypes into groups, given user-specified primary and null hypotheses. We specified a primary hypothesis of haplodiploid full siblings to compare with a complex null hypothesis including 40 search intervals between nonrelatives and parents–offspring.

To assess the number of breeders in the colony, we first manually inspected brood genotypes to roughly assess whether multiple matrilines were present. A typical *Polistes* foundress is effectively singly mated (Strassmann 2001) and therefore produces female offspring that share the same paternal allele and one of two maternal alleles. We then calculated pairwise and group relatedness and used KinGroup with the same settings as described above except the null hypothesis included 20 search intervals between nonrelatives and maternal half-siblings. Finally, we searched within the sample of adult females for genotypes that were consistent with having produced the resulting sibling groups.

## Reproductive Tract Dissections

To assess ovarian development, we dissected reproductive tracts of 22 adult females using insect pins under a stereomicroscope. We noted the presence of yellow bodies (an indicator of previous egg laying) and inspected the ovarioles for the presence of mature oocytes. We also used dial calipers to measure the head widths of all dissected females as an indicator of body size. Using DataDesk 6.2, we then performed a Mann-Whitney $U$ test to compare females with undeveloped vs. developed ovaries.

## Results

### The Nest

The nest contained 613 cells, of which 536 (87.4%) held live brood, 63 were empty, 11 had dried, shriveled brood, and three contained a combination of honey droplets and meconia (the pellet defecated prior to eclosion). There were also 19 cells with tandem brood (more than one egg, larva, or pupa per cell), and many cells with live

brood also had meconia and/or honey. All developmental stages were present in each quadrant of the nest; of 555 brood, 18.2% were eggs, 4.1% L1, 12.8% L2, 17.5% L3, 24.1% L4, and 23.2% pupae.

The Adults

Of the 84 adults collected, 80 were females and four were males. Genotypes were successfully obtained from all adults at a minimum of five loci, and from 95% at six or seven loci. Of the four males, three were haploid and one diploid (heterozygous at four of seven loci).

Inspection of the adult genotypes clearly eliminated the possibility that all 80 females were full or half siblings, although smaller subgroups appeared to share alleles in the pattern consistent with full and half sisters, and at least one subgroup of nine females may have been the daughters of another adult female.

Two different algorithms available in the program KinGroup were used to partition the sample of 80 adult female genotypes into the set of full sibling groups with the greatest likelihood relative to the null hypothesis (Konovalov et al. 2004). The descending ratio (DR) algorithm found 12 sibling groups with group sizes ranging from 2 to 14 females (median=3), accounting for 73 females in total. The exhaustive descent (ED) algorithm found slightly different results: 13 groups, with sizes ranging from 2 to 22 (median=5.5), including a total of 76 females (Table 1). The inconsistent results between the two algorithms may reflect relatively low allelic diversity at some loci (Table 2), which allowed for multiple possible groupings. The low allelic diversity also prevented us from distinguishing among kin relationships on a finer scale; unfortunately, we were therefore unable to assign individuals unambiguously to mother-offspring, cousin, or half-sibling groups. However, the overall adult female relatedness value of 0.26±0.263 (mean±95% CI) indicates that the sample did not consist of uniformly close relatives. Moreover, 42.9% of 3,160 pairwise relatedness values were less than 0.1875, which is the expected value for maternal cousins.

Reproductive tract dissections of 22 adult females revealed ten that had stringy ovarioles with no measurable oocytes, while 12 females had mature, measurable oocytes in their ovarioles. Yellow bodies were also observed in five of 12 females with developed ovaries, indicating that these females had already laid eggs. Females with undeveloped ovaries may have been subordinate, nonbreeding foundresses; alternatively, some may have been recently eclosed offspring. In many *Polistes*

**Table 1** Sibling Group Partitioning Results Obtained from the Program Kingroup for Female Adults and Brood

|  | Adults-DR[a] | Adults-ED | Brood-DR | Brood-ED |
|---|---|---|---|---|
| Number of groups | 12 | 13 | 11 | 10 |
| Minimum size of groups | 2 | 2 | 2 | 2 |
| Maximum size of groups | 14 | 22 | 4 | 7 |
| N (%) of sample in groups | 73 (91%) | 76 (95.0%) | 38 (82.6%) | 29 (63.0%) |

*DR* Descending ratio, *ED* exhaustive descent

[a] The results of two different algorithms are presented for each sample

**Table 2** Number of Alleles Per Locus for Three Different Samples

| Locus | Number of alleles per locus | | | Total alleles per locus |
|---|---|---|---|---|
| | Adults (*N*=80) | 2N brood (*N*=46) | 1N brood (*N*=39) | |
| Pdom 117 | 6 | 7 | 3 | 7 |
| Pdom 122 | 7 | 7 | 2 | 9 |
| Pdom121 | 5 | 7 | 2 | 7 |
| Pdom 1 | 4 | 5 | 5 | 5 |
| Pdom 140 | 6 | 7 | 4 | 7 |
| Pdom 127b | 5 | 6 | 4 | 6 |
| Pdom 25 | 5 | 5 | 3 | 6 |
| Mean | 5.4 | 6.3 | 3.3 | 6.7 |
| SD | 0.98 | 0.95 | 1.11 | 1.25 |

species including *P. dominulus*, the earliest emerging female offspring are smaller than foundresses and later-emerging offspring (Reeve 1991). As an indicator of body size we compared head widths among females with undeveloped vs. developed ovaries. The wasps with developed ovaries (Mean±SD: 3.03±0.10, *N*=12) had significantly larger head widths than females with undeveloped ovaries (2.83±0.12; *N*=10) (Two-tailed Mann-Whitney *U* Test: *U*=70, *P*=0.0006).

The Brood

Of 96 brood from which DNA was isolated, 80 (83.3%) were successfully genotyped at five or more loci, with an additional 5 (5.2%) at four loci. The remaining 11 samples with genotypes at fewer than four loci were excluded from further analysis. Of these 85 brood, 54.1% (*N*=46) were diploid (thus "intended" as females, though diploid males sometimes occur; Liebert et al. 2005b) and 45.9% (*N*=39) were haploid males. Of the 39 haploid males, 74% were young (egg-L3) and 26% were old brood (L4-pupae). Of the diploid brood, 62% were old and 38% young. The majority (62%) of the young brood and only 25% of the old brood were haploid males.

If a single diploid foundress had mated with one haploid male, we would expect only three shared alleles at each locus and an average relatedness value of 0.75 among the 46 female (diploid) brood. In contrast, genotype data revealed more than three alleles at all loci (Table 2) and overall relatedness of female brood was 0.22± 0.20 (mean±95% CI). This suggests either the presence of multiple breeders or of multiple mating, though the latter is not commonly observed in this species. Evidence for multiple breeders is shown by the fact that 44.5% of 1,035 pairwise relatedness values for the female brood were lower than 0.1875, as well as by the KinGroup results. The DR partitioning algorithm found 11 full sibling groups that ranged in size from 2 to 4, and included 38 of 46 individuals. Once again the ED algorithm produced slightly different results: ten full sibling groups, with group size ranging from 2 to 7, and including 29 individuals. These putative sibling groups were not clustered by area of the nest; each group contained offspring from multiple nest quadrants. Thus, the nest did not appear to be divided into separate sub-regions headed by different foundresses. We attempted to match these putative sibling groups with expected maternal genotypes from among the adult females. However,

low allelic diversity among the samples made unique maternity assignments impossible in all but one case.

Of the 19 tandem brood cells, nine were double eggs, six had eggs and larvae, one had an egg and pupa, and three had double larvae. Thus, 92.1% ($N=35$) of these were young brood. Data from the 18 tandem pairs we genotyped suggested that 66.7% ($N=24$) were haploid males and the remaining 33.3% ($N=12$) were (presumably female) diploids. The tandem brood cells were evenly spread out throughout all four quadrants of the nest ($X^2=4.53$, $df=3$, $P>0.1$), indicating that this atypical egg-laying behavior was not relegated to one differentiated area of the nest.

## Discussion

The presence of meconia and dried, shriveled larvae support the observation that this was a reused nest. As mentioned previously, *Polistes* wasps do not commonly reuse nests. In areas where nests are exposed to weathering, reuse may be impossible. Where nests remain intact, reuse is thought to be infrequent due to the risk of residual parasitism (Yamane 1996), as some parasites overwinter in empty nests (e.g., *Chalcoela iphitalis*; Strassmann 1981). Strassmann (1983) also pointed out that in *P. annularis*, reused nests are more likely to mold and to become large and heavy, leading to greater risk of detachment.

Nevertheless, nest reuse has been observed in *Polistes* species including *P. dominulus* in its native range. Cervo et al. (2000) suggested that this behavior allows foundresses to save time and resources at the beginning of the nesting season. Indeed, our data suggest that this reused colony had already produced workers as well as a few early males at the time of collection at the start of May, and so had already entered the growth or worker phase of the colony cycle while typical *Polistes* colonies in this area remained in the founding phase (Liebert et al. 2005a).

Another potential benefit of nest reuse is that resident females may have greater opportunities for direct reproduction. The rare reports of such nests in other *Polistes* species provide evidence in support of this idea. Cumber (1951) dissected 214 females from one large reused *P. humilis* nest collected in the summer from Paihia, Bay of Islands, New Zealand and found 87 (40.7%) with countable eggs in their ovaries. For another reused *P. humilis* nest in Brisbane, Australia, Itô (1986) observed oviposition by six of over 20 resident females, found mature eggs in 74% of dissected females, and reported generally low aggression or signs of dominance behavior. Strassmann (1983) also observed greater egg-laying rates by subordinates in larger foundress associations of *P. annularis*, and suggested that the chance for direct reproduction might outweigh the risks of nest reuse. This pattern of increasing proportion of breeders with group size has also been recently demonstrated in *P. dominulus* (Cant and English 2006), although here the authors posit that large group size is a result, not a cause of increased breeding opportunities. They assume, however, that dominant females are fully capable of patrolling the nest to maintain control over reproduction, and this may not be the case for the large nest size of a hypergynous colony.

The adult genotype data from this study are consistent with the idea that our sample contained some recently eclosed offspring. However, it is clear that, like the

examples above, a large number of females were actively breeding in the colony. This is supported by the ovarian development data, which revealed more than half (12) of the 22 dissected females to have developed ovaries, five of which actually had yellow bodies as evidence of previously laid eggs. The presence of multiple breeders is also indicated by the low relatedness and KinGroup data for 46 female brood, which could not be partitioned into fewer than ten sibling groups. Because this sample represented only a fraction of the adults and brood, it is most likely an underestimate of the number of egg-layers on the nest. As such, these results provide evidence for one of the largest groups of actively breeding females within a cooperative nesting association that, to our knowledge, has ever been documented in *Polistes* wasps.

The occurrence of multiple breeders is not surprising, given that behavioral dominance by one or two foundresses would be extremely difficult to maintain within such a large group. Without foundress control, emerging female offspring might be able to avoid working and lay eggs instead. The fact that 62% of young brood was male also suggests that this may have been the case, although it is also possible that some foundresses were also uninseminated due to a scarcity of males in this recently established, low-density population. The presence of at least one diploid male may also indicate the difficulty of finding unrelated mates.

The tandem brood, consisting primarily of male-destined eggs, provide further evidence for the lack of control over reproduction. In the honey bee *Apis mellifera*, cells with multiple brood signify loss of queen control and the onset of a chaotic state that soon leads to colony decline (Winston 1987). This phenomenon is also known in perennial polygynous *Vespula* colonies, where as many as 17 eggs have been observed in one cell (Spradbery 1991). Tandem brood have been observed in *Polistes*; as cited by Rabb (1950), Rau (1929) observed two eggs per cell but described the phenomenon as extremely rare, due to the lack of reports of two larvae developing in a single cell. This report is the first to our knowledge to include double larvae, although we suspect only one per cell would eventually survive to pupation.

Interestingly, despite these signs of "chaos", the colony appeared to be highly productive. The roughly equal proportions of young and old brood demonstrate that larvae were being cared for continuously. Nest residents must therefore have been actively foraging until the time of collection. This high level of productivity was also observed for a different hypergynous colony in the same location the following year (P. Nonacs, pers. obs.). The question of how this productivity is maintained in such a large colony remains unanswered.

This study of one hypergynous colony clearly is not a comprehensive analysis of this unusual phenomenon, but it raises some interesting questions about the relationship of group size, productivity, and regulation of nest activity in *P. dominulus*. As this species continues to spread in its introduced range (Liebert et al. 2006), opportunities for further study of hypergynous colonies are likely. Additional studies will help expand these preliminary findings to shed light on whether the results reported here are typical of this phenomenon in *P. dominulus*.

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