Natal nest discrimination in the paper wasp, *Polistes dominulus*

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I present data indicating that *Polistes dominulus* females overwinter in multi-colony groups, recognize natal nest fragments after overwintering, and select nesting cavities based on cavity volume. In a seminatural environment, seven field-captured *P. dominulus* colonies completed the colony cycle, and the resulting reproductive females were observed in hibernacula groups, on natal nest fragments prior to colony initiation, and in nest boxes after initiating colonies. Given the choice of three nest box sizes in which to initiate colonies, *P. dominulus* preferred medium nest boxes and avoided large nest boxes. This site preference may indicate a balance between the cost of detection by predators and the benefit of space for colony growth. Even though natal nests were cut into small fragments and distributed into nest boxes, spring foundresses recognized and preferentially perched upon fragments from their natal nest. Individuals whose natal nest contained multiple queens were significantly more likely to perch upon natal nest fragments than were individuals whose natal nest contained a single queen. Returning to and recognizing the natal nest may be an adaptive mechanism to (A) locate nestmates with whom to initiate multiple foundress colonies and (B) reduce the cost of finding these nestmates.

Introduction

Systems in which adults breed cooperatively have generated significant interest with behavioral ecologists (Vehrencamp 1983a, 1983b). Specifically, questions relating to the degree that reproduction is shared (i.e., reproductive skew) within cooperative societies have given rise to theoretical explanations for the evolution of eusociality as well as a great number of empirical studies testing these hypotheses (reviewed in Keller & Reeve 1994, Clutton-Brock 1998, Johnstone 2000, Reeve & Keller 2001, Nonacs 2001). A majority of these studies have been performed on social insects, with the most detailed performed on *Polistes* wasps (Reeve & Keller 2001). This bias is not surprising because *Polistes* have been a favorite study organism for behavioral ecologists since the early work of Leo Pardi in the 1930s (reviewed in Pardi 1996). These eusocial insects display slight caste differentiation and multiple colony founding strategies, and are thus ideal for the study of reproductive conflicts of interest, nepotism, and

the evolution of sociality (reviewed in Reeve 1991, Turillazzi & West-Eberhard 1996).

Reproductive females (gynes) in temperate species mate in the fall and overwinter in hibernacula groups (West-Eberhard 1969). In spring, gynes emerge from hibernacula as foundresses, return to their natal site, and initiate colony construction (Rau 1929, West-Eberhard 1969, Strassmann 1983). A wasp may found a colony singly, join a conspecific in a multiple foundress association, usurp an initiated colony, or wait to adopt an orphaned colony (Reeve 1991, Nonacs & Reeve 1993, Starks 1998, 2001). Foundresses that cooperate in the construction of a nest are naturally the focus of reproductive skew studies. Studies have shown that co-foundresses are not always genetically related (Queller *et al.* 1990, 2000, Reeve *et al.* 2000), as would be expected due to the potential for kin-selective benefits (Hamilton 1963, 1964a, 1964b).

This observation is even more curious since foundresses, fall reproductives, and workers in virtually all examined *Polistes* species display nestmate and/or nest-material discrimination (reviewed in Gamboa 1996). Previous evidence strongly suggests that the extent of discrimination is dependent on the social and environmental context to which a wasp is exposed (Gamboa *et al.* 1991, Fishwild & Gamboa 1992, Venkataraman & Gadagkar 1992, Starks *et al.* 1998, Starks 1999, Pickett *et al.* 2000). Since kin-selective benefits are maximized when full sisters cooperate (Hamilton 1963, 1964a, 1964b), a critical time for nestmate discrimination occurs prior to forming a multiple foundress association (Strassmann 1996). Although multiple foundress associations are sometimes between unrelated individuals (Queller *et al.* 1990, 2000, Reeve *et al.* 2000), extensive evidence suggests that spring females are likely to found colonies with relatives (Metcalf & Whitt 1977, Klahn 1979, Reeve *et al.* 2000).

Spring foundresses appear to have a mechanism for locating relatives with whom to initiate a colony. One potential mechanism is for wasps to return to the natal nest after overwintering (*see* Wenzel 1989, 1996) and then form associations with other returning females. Indeed, it has long been observed that overwintered females are philopatric (Rau 1929, West-Eberhard 1969,

Strassmann 1983, but *see* Reeve *et al.* 1998). Although *Polistes* wasps commonly return to the natal nest site and both worker and reproductive wasps recognize familiar nest fragments in the laboratory (Ferguson *et al.* 1987, Espelie *et al.* 1990, Pfennig 1990, Starks *et al.* 1998, Starks 1999, Lorenzi & Caprio 2000), it has yet to be demonstrated, in a natural environment, whether spring foundresses recognize the natal nest *per se* or simply return to the natal site.

I examined (A) whether overwintered *P. dominulus* females recognized natal colony nest fragments independent of the natal site's surrounding landmarks, and (B) if individuals raised on single versus multiple foundress colonies were more or less likely to return to fragments of their natal nest. The relevance of the latter question arises due to the observation that relatedness between co-founding natal nestmates is not significantly greater than between natal nestmates in general (reviewed in Strassmann 1996). Since these animals do not seem to display intra-colonial kin discrimination, cooperative associations between nestmates whose natal colony contained multiple reproductive females may lead to associations between unrelated wasps (Queller *et al.* 2000).

After allowing field-collected colonies to mature in an unheated greenhouse, I collected nests abandoned when the gynes entered hibernacula. The nests were divided into fragments and distributed in nest boxes of various sizes within the greenhouse. I located nine hibernacula groups and censused all overwintering animals. Observations were taken of individuals that, after leaving hibernacula, visited nest fragments during the pre-founding phase. Associations between individuals and nest fragments served as an indicator of natal nest preferences. As a consequence of this evaluation, I examined the colonial make-up of hibernacula groups and preferences in colony initiation.

The question of colony initiation is of significant interest due to the rapid and successful invasion of the United States by *P. dominulus* (Cervo *et al.* 2000, Gamboa *et al.* 2002). Multiple hypotheses have been suggested for the success of the invasion including *P. dominulus'* versatile diet, its ability to colonize previously unused nesting sites, its resemblance to the
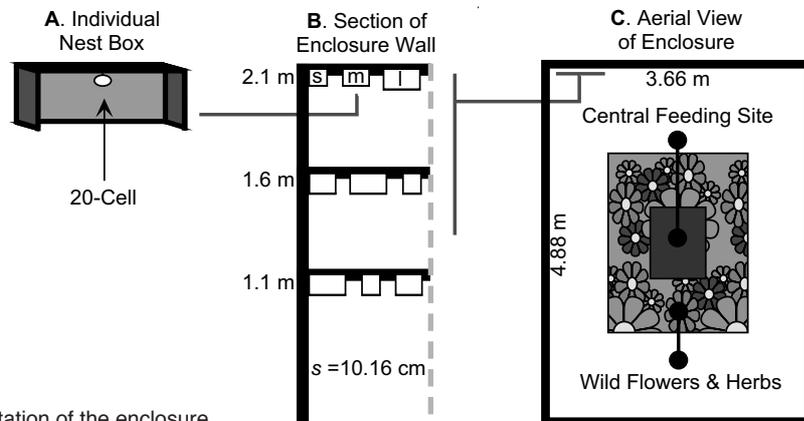
Fig. 1. Schematic representation of the enclosure.

highly aggressive *Vespula germanica*, and its propensity for nesting in sheltered areas (Cervo *et al.* 2000). This latter hypothesis can be examined directly: by providing *P. dominulus* with multiple possible nesting sites, preferences for more sheltered locations can be assessed.

Methods

In August 1995, seven colonies (nest and wasps) of *Polistes dominulus* were collected from Carlisle, MA (42°21′N, 71°2′W; $N = 3$ colonies) and Ithaca, NY (42°27′N, 76°29′W; $N = 4$ colonies). These colonies were easily located due to their location: all were constructed in the eaves of man-made structures. Collected colonies were transplanted into open-face cardboard boxes (76.2 cm × 45.7 cm × 15.2 cm) located in the center of a metal frame screen enclosure (2.44 m × 2.44 m × 2.14 m) which itself was within an unheated and unshaded greenhouse at Cornell University's Liddell Field Station. Multiple foundress colonies were transplanted from both Carlisle ($N = 2$) and Ithaca ($N = 2$); all remaining transplanted colonies were single foundress colonies. Single and multiple foundress status was determined through census information gathered in May and June 1995. Colonies were collected from widely separated areas to ensure a sample of unrelated colonies.

All transplanted wasps and many of the reproductives that eclosed after transplantation were given colony-specific thoracic marks with Testors enamel paint prior to entering hibernac-

ula. Between December 1995 and March 1996, I located nine naturally formed hibernacula groups as the wasps overwintered. Hibernacula groups were located between sections of cardboard. Individuals in hibernacula with colony-specific marks ($N = 89$) were censused and all located overwintering animals ($N = 229$) were marked with numbered bee tags. Unfortunately, many numbered bee tags did not remain secured and a number of animals (~70) did not survive the winter.

While the wasps overwintered, the metal screen enclosure was removed and a larger wooden frame screen enclosure (4.88 m × 3.66 m × 2.14 m) containing 120 nest boxes was built around the hibernacula sites (Fig. 1). Three sizes of open-face plywood nest boxes ($N = 40$ each), differing in length (10.16 cm, 20.32 cm, and 40.64 cm) but of consistent depth and height (10.16 cm × 10.16 cm; Fig. 1A), were attached to the frame of the enclosure at three heights within the natural range of nest heights: 1.1 m, 1.6 m, and 2.1 m (Fig. 1B). Prior to foundress emergence, each of the natal combs ($N = 7$) and three unfamiliar *P. dominulus* combs collected in Ithaca, NY were divided into six 20-cell fragments and attached by pin to an upper back corner in 60 of the 120 nest boxes. The nest fragments contained no brood. Fragments were distributed to nest boxes in a randomized block design such that each natal nest contributed fragments attached in nest boxes on each of the four walls of the enclosure, in each size of nest box, and on each of the three nest box heights. Care was taken to ensure that fragments were not

clumped and that fragments from the same nest were not adjacent to each other. After leaving hibernacula, the wasps were provisioned with water, honey-water, and mealworms located at a central feeding site. To simulate natural conditions, the enclosure contained a variety of flowering plants (Fig. 1C). Wasps were observed to forage and interact with conspecifics.

Nest boxes were censused nightly between 21:30 and 23:30 from 6 May 1996 through 15 June 1996. Census information was gathered on marked individuals located in nest boxes. Wasps with both individual and colony-specific marks that perched on nest fragments (N = 65) were used in the natal nest-fragment association study. If an individual was located on the same fragment on consecutive nights ($\geq$ 2 nights), it was counted as a single observation in the natal nest preference data analysis. This estimate of preference is conservative since four of the five wasps located on the same nest fragment on consecutive nights were perched on natal nest fragments. Observations of wasp-nest fragment associations ceased when the first nest construction began (13 May 1996).

Observations of nest construction ceased after seven consecutive days during which no new construction occurred (15 June 1996). Fifty-seven wasps initiated 42 colonies, 14 (33%) of which were multiple foundress associations. This frequency of multiple foundress associations closely matches the frequency observed in the Ithaca area and the density of enclosure nests was within the natural range of nest densities (P. Starks, unpubl. data). Thirty-four colonies were initiated within nest boxes; the remaining eight colonies were located between nest boxes (N = 2), above nest boxes (N = 3), or on the wooden base of a central feeding apparatus (N = 3).

Descriptive statistics are represented as means ± standard error. Data on nest box choice were analyzed with binomial and chi-square tests. Data on natal nest fragment association were analyzed with binomial tests, chi-square tests and, when comparing preferences between individuals raised on multiple foundress versus single foundress colonies, a non-parametric two-tailed Mann-Whitney test. Data on the latter were standardized prior to analysis by subtracting the expected number of associations from the observed number of associations and dividing that value by the expected value.

Results

Hibernacula associations

Polistes dominulus gynes overwintered in multi-colony hibernacula groups. Nine hibernacula groups were located and examined. The mean number of individuals per association was 25.44 ± 5.47 (range 8 to 54) and the mean number of colonies represented in each hibernacula group was 3.89 ± 0.42 (range 2 to 6). A positive linear relationship between the number of individuals in a hibernacula group and the number of different colonies represented within the group was observed (r^2 = 0.62, df = 8, P < 0.01).

Natal nest fragment association

P. dominulus foundresses displayed a strong preference for perching on fragments of their natal colony (binomial test: 17 observed, 6.5 expected, P < 0.001; Fig. 2). Individuals that were raised on multi-foundress colonies were more likely than those raised on single foundress colonies to associate with natal nest fragments (Mann-Whitney test: n_1 = 4, n_2 = 3, U = 12.0, P < 0.05; Fig. 2). Differences in natal nest association were not observed with respect to origin of collection (NY vs. MA; χ^2_1 = 0.059, P > 0.750).

Nest box preference

Colonies were not initiated randomly with respect to nest box size (χ^2_2 = 13.12, P < 0.005). Wasps preferred medium nest boxes (binomial test: P < 0.01) and avoided large nest boxes (P < 0.001; Fig. 3). No significant effect of nest box height (χ^2_2 = 0.77, P > 0.50), compass direction (χ^2_3 = 1.53, P > 0.75), or presence versus absence of a nest fragment (χ^2_1 = 1.47, P > 0.25) was observed. For the initiation of a new nest, cooperating females (i.e., those in multiple foun-
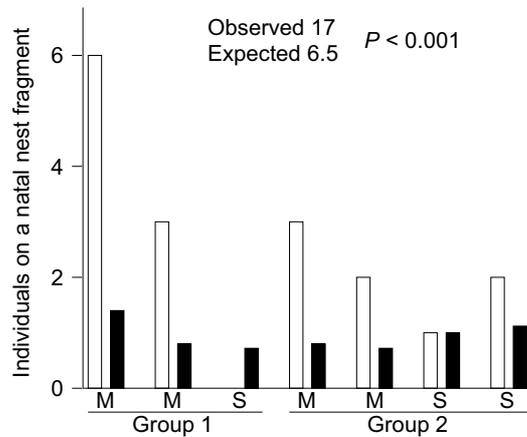
Fig. 2. Comparison of the observed (□) and expected (■) number of spring foundresses associating with familiar natal nest fragments. 'M' signifies that the natal colony was founded by multiple females and 'S' signifies that the natal colony was founded by a single female. A lack of a '□' signifies that no animals were observed perched upon fragments of their natal nest. Group 1 natal colonies were collected in Carlisle, MA and Group 2 natal colonies were collected in Ithaca, NY. The expected number of associations was calculated by multiplying the probability of randomly associating with a familiar nest fragment ($P = 0.10$) with the number of individuals from a given colony observed perched on any nest fragment.
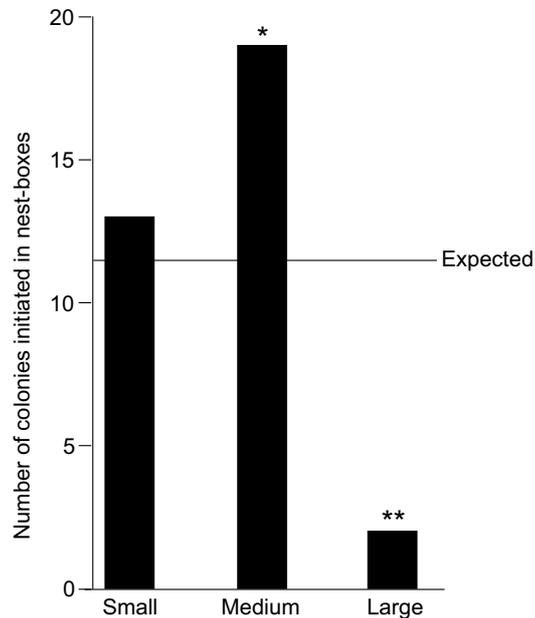

Fig. 3. Comparison of the observed and expected number of colony initiations in nest boxes of different sizes. Wasps preferred medium nest boxes and avoided large nest boxes. The probability of randomly founding in a small, medium, or large nest box was 0.33, $N = 34$, $* = P < 0.01$, and $** = P < 0.001$ binomial test.

dress associations) did not differ from single foundresses in the preference for size of nest box or presence of a nest fragment.

Discussion

In a seminatural environment, *Polistes dominulus* females overwintered in multiple colony groups, recognized natal nest fragments, and selected nesting sites based on cavity size. With respect to the latter, foundresses preferred to initiate colonies in medium sized nest boxes and appeared to reject large nest boxes (Fig. 3). Since there were no founding preferences besides nest box size and since the environment was completely new (i.e., constructed around the hibernating wasps), it seems unlikely that an unmeasured characteristic, which correlated with nest box size, was the actual determining factor in nest site selection. Other factors, such as thermal properties (Jeanne & Morgan 1992), will naturally play a role in the wild but did not seem to play a significant role

even though a temperature gradient within the enclosure likely existed (Starks 2001).

This nest site preference suggests that an optimum cavity size for colony initiation may exist. Individuals may balance the cost of detection by predators with the benefit of colony expansion. Indeed, *Polistes* colonies are attacked by many predators (reviewed in Yamane 1996) and large predators (i.e., birds) frequently destroy exposed, naturally founded *P. dominulus* colonies (Nonacs & Reeve 1995). Thus, these results provide partial support for the hypothesis that the rapid and successful invasion of the United States by *P. dominulus* is aided by the animal's propensity for nesting in sheltered areas (Cervo *et al.* 2000). Observations of founding behavior within the enclosure support an additional hypothesis raised by Cervo and colleagues (2000) for *P. dominulus*' successful invasion: spring foundresses not only colonized a new environment, but did so by constructing nests on a variety of surfaces (within nest boxes, between nest boxes, and on the central feeding site). Future analyses should

compare founding behavior between *P. dominulus* and *P. fuscatus*, the native wasp sympatric with *P. dominulus* in this study area. Since the observations reported here were from an isolated population of *P. dominulus,* these data cannot be used to show a competitive advantage based on nest site selection alone.

Consistent with reports that overwintered females return to the natal colony (Rau 1929, West-Eberhard 1969, Strassmann 1983), spring foundresses exhibited a preference for perching on natal nest fragments (Fig. 2). Since the site of origination (NY or MA) did not influence this propensity, natal nest recognition appears common to *P. dominulus*. However, this propensity was influenced by the founding strategy exhibited on the natal nest. Individuals who were raised on multiple foundress colonies were significantly more likely to perch on natal nest fragments than were individuals raised on single foundress colonies (Fig. 2). Assuming that pre-nest initiation associations lead to cooperative nest founding, these data raise the possibility that individuals from multiple foundress colonies are more likely to cooperate in nest founding than are individuals from single foundress colonies. Due to the small number of colonies examined, however, this result should be viewed with caution.

The screen enclosure in which the natal nests were transferred was removed while the wasps overwintered. The females overwintered between sections of cardboard away from their natal nests in multiple colony groups (West-Eberhard 1969). The natal nests were then divided into 20-cell fragments, distributed to nest boxes within the enclosure, and the original cardboard boxes containing the natal nests were removed. As such, no non-nest natal landmarks remained and the wasps did not have the option of returning to the exact site where their natal nest was originally transplanted and where many of them eclosed as adults. Since natal nest site is a strong determinant of nest site choice (Wenzel 1989, 1996), these wasps were forced to found nests on unfamiliar surfaces.

The discriminating wasps must have examined and recognized nest fragments prior to perching on a natal nest fragment. Since the fragments no longer resembled the natal nest (i.e., the nests were cut into small fragments), these results suggest that *P. dominulus* females use chemical cues (Singer & Espelie 1996, Lorenzi & Caprio 2000) rather than strictly spatial or visual cues to return to the natal comb. Indeed, recent evidence suggests that *P. dominulus* will not discriminate in favor of nest material that has had the signature hydrocarbons extracted (Lorenzi & Caprio 2000). Since *Polistes* colonies are often found in areas with high population densities (Gamboa 1978, Wenzel 1989), recognizing colony chemical cues would be advantageous in that once the animal returns to the general site it could more precisely locate its nest.

Polistes wasps may return to their natal site for numerous reasons. For example, it may be advantageous to return to a known successful site and the presence of old combs may be an indicator of recent nesting success and site quality (Wenzel 1996). The absence of a preference for initiating colonies in nest boxes with nest fragments ('old combs') presented here is not evidence against this hypothesis. As a natal site may encompass many potential nesting sites, failure to found a nest immediately next to an old comb does not suggest that the presence of the old comb was not an indicator of site success.

Returning to the natal nest prior to colony initiation may also be advantageous in maximizing kin selective benefits. After overwintering in multi-colony groups, associating with nestmates on the natal nest prior to colony initiation may be a mechanism to minimize errors in nestmate recognition, which could lead to colony founding with non-nestmates. Although laboratory experiments indicate that *P. dominulus* can discriminate between nestmates and non-nestmates in the absence of nest material, the presence of familiar nest material increases the amount of aggression directed at non-nestmates (Starks *et al.* 1998). As such, returning to the natal nest may enhance discrimination abilities while simultaneously reducing the cost of searching for nestmates.

Natal nest fidelity may be a stage in the early nesting cycle that partially explains both nonrandom foundress associations (reviewed by Reeve 1991) and the lack of within-colony nepotism (Queller *et al.* 1990, Hughes *et al.* 1993). Individuals returning to their natal nest prior to nest initiation are likely to interact with nestmates

with whom they may jointly found a colony, thus explaining the higher level of relatedness within foundress associations than expected by chance. However, spring foundresses interacting on their natal nest need not be from the same matriline (but *see* Quellar *et al.* 2000). Data presented here raises the possibility that individuals raised on colonies with multiple matrilines may be more likely to return to the natal nest than individuals raised on colonies containing a single matriline (Fig. 2). In the absence of intra-colonial kin discrimination, natal-nestmate spring foundresses who cooperate in multiple foundress associations and whose natal colony contained multiple matrilines may not be more closely related than were the foundresses on the original colony. Hence, the presence of nestmate, but not exclusively full-sister, multiple foundress associations may be partially explained by associating with nestmates on the natal nest prior to colony initiation. This hypothesis, however, is specific to interactions occurring on the natal nest *prior* to colony initiation and does not address the issue of foundress associations formed away from the natal nest after the initiation of nest construction.

Conclusions

I have presented the first evidence that over-wintered spring foundresses in *P. dominulus* exhibit natal nest recognition under seminatural conditions and that individuals from multiple foundress colonies are more likely to return to the natal nest fragment than individuals from single foundress colonies. I propose that returning to the natal nest is a mechanism to (A) limit recognition errors and thus increase the chances of co-founding with nestmates rather than non-nestmates and (B) reduce the cost of finding such nestmates. Finally, preliminary evidence suggests that *P. dominulus* may be acting optimally in choosing nest cavities, possibly balancing the cost of detection by predators with the benefit of colony expansion. Thus, these results provide partial support for the hypothesis that the rapid and successful invasion of the United States by *P. dominulus* is aided by the animal's propensity for nesting in sheltered areas (Cervo *et al.* 2000).

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