



A novel 'sit and wait' reproductive strategy in social wasps

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I present evidence indicating that a subset of spring females in the social wasp *Polistes dominulus* do not initiate colonies but rather 'sit and wait' to adopt colonies initiated and abandoned by other conspecifics. These results are, to my knowledge, the first to demonstrate conclusively this alternative reproductive strategy in social wasps. Individuals engaging in the sit-and-wait strategy behave selfishly by adopting the most mature nests available; such nests will produce workers sooner than less mature nests and, consequently, are more likely to survive. The sit-and-wait reproductive strategy may safeguard an individual from early-season, foraging-related mortality as well as reduce early-season energy expenditure.

Keywords: paper wasps; *Polistes dominulus*; reproductive strategies; founding behaviour

1. INTRODUCTION

In the spring, females of the paper wasp, *Polistes dominulus*, are known to display several colony-founding behaviours (Reeve 1991; Turillazzi & West-Eberhard 1996). Overwintered females can initiate colonies as single foundresses, form associations with other females (i.e. co-found colonies), usurp established colonies from other foundresses, or adopt abandoned nests. Wasps likely to usurp or adopt colonies have either lost their colonies (reviewed in Cervo & Dani (1996)) or are subordinates on multiple-foundress colonies who leave the association to assume dominant status on a new nest (Nonacs & Reeve 1993). Usurpers and adopters typically destroy the previous foundress's eggs and early instar larvae and replace them with their own eggs (Klahn 1988). The older larvae and pupae are allowed to complete development and then work to raise the new queen's offspring (Klahn 1988).

Within a population of marked foundresses, Nonacs & Reeve (1993) observed 21 unmarked wasps each adopt one of 72 newly abandoned or transplanted nests. They suggested that these individuals had not left established colonies, but rather had delayed colony founding to wait for the opportunity to secure an orphaned nest (Nonacs & Reeve 1993). Thus, they hypothesized, some *Polistes* wasps may conserve the energy normally spent in colony founding and instead 'sit and wait' to reap the benefits of another wasp's early reproductive efforts.

Identifying adopters as individuals who have lost their original nests or who were once subordinates on multiple-foundress nests is not problematic; it requires only that foundresses are distinctively marked and that reliable census information is taken (Nonacs & Reeve 1993, 1995). However, confirming the sit-and-wait strategy in the field has been very difficult owing to the possibility that adopters were foundresses on cryptic or distant nests. I have examined this hypothesis in a semi-natural environment, where I induced adoption of

abandoned nests and identified the adopters and the nest characteristics attractive to adopters.

2. METHODS

In August 1995, seven colonies of *Polistes dominulus* were collected from Carlisle, MA ($n=3$ colonies) and Ithaca, NY ($n=4$ colonies) and transplanted into a metal-frame screen enclosure (2.44 m \times 2.44 m \times 2.14 m) housed within an unheated greenhouse at Cornell University's Liddell Field Station. While the wasps overwintered, a larger wooden-frame screen enclosure (4.88 m \times 3.66 m \times 2.14 m) was built to replace the metal-frame screen enclosure. Three sizes of open-face nestboxes ($n=40$ each), differing in length (10.16 cm, 20.32 cm and 40.64 cm) but of consistent depth and height (10.16 cm \times 10.16 cm), 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. In 60 of the 120 nestboxes, a 20-cell nest fragment, containing no brood, was attached by a pin to the upper back corner. The distance between nestboxes within the enclosure was similar to the mean inter-nest distance within nest aggregations in the Ithaca area (P. T. Starks, unpublished data). To mimic natural conditions, the enclosure contained six varieties of naturally occurring flowering plants and 12 varieties of herbs.

After the wasps left hibernacula in early May 1996, they were provisioned with water, honey-water and meal worms. Between 13 May 1996 and 8 June 1996, 57 wasps initiated 42 colonies, 14 of which were multiple-foundress associations. This frequency of multiple founding closely resembles the frequency observed in natural populations within the Ithaca area (ca. 30%; P. T. Starks, unpublished data). All 57 foundresses either had marks from the previous fall or were given distinctive thoracic marks with Testors enamel model paint. Wasp behaviour appeared normal: individuals foraged, initiated nests, oviposited and fed larvae. Wasps preferred to found nests in medium-sized nestboxes and avoided larger ones. The presence of a nest fragment or the location of the nestbox had no impact on founding preferences (Starks 1998). Thus, all locations appeared

suitable for nest initiation. All nests were easily located and the enclosure was censused daily.

On 24 June 1996, 35 pre-worker phase *P. dominulus* nests, collected from four sites in the Ithaca area, were attached to empty nestboxes using wood glue and a pin anchor. Care was taken to ensure that adoptable nests were not placed in large nestboxes or in nestboxes adjacent to naturally founded nests. The adoptable nests were similar to the nests founded in the enclosure in both size and development. The distances between the sites where the transplanted colonies (wasps and nests) were gathered in 1995 and the sites where the adoption-destined nests were located in 1996 was 10–600 km. Thus, I assume that adopted nests were initiated by conspecifics unrelated to the adopters.

All queens were removed from the 35 adoptable nests and the number of cells, eggs, larvae and pupae were recorded for each nest. Based on size and head capsule width, larvae were assigned to one of two groups: (i) first, second and third instar larvae or (ii) fourth and fifth instar larvae. These queenless, and thus adoptable, nests were censused nightly until all adoptions ceased (on 26 June 1996).

An overall nest maturity score was calculated for each nest. Pardi (1951) determined the mean developmental time an individual of *P. dominulus* (misidentified as *P. gallicus*; see Reeve (1991)) remains in each developmental stage (Strassmann & Orgren 1983, table 6), and these means were used to set the interval scale of each stage in the maturity score. The interval scale consisted of the average time an individual brood needed to reach the end of a particular stage, standardized by the developmental period of an egg. Thus, a weighted average was calculated by multiplying the number of pupae by 3.90 (39 days), the number of fourth and fifth instar larvae by 2.60 (26 days), the number of first, second and third instar larvae by 1.96 (19.6 days) and the number of eggs by 1.00 (10 days); these values were then summed and this result was divided by the total number of nest cells.

Individuals who remained on and defended a newly transplanted, unfamiliar nest for longer than a single day were identified as adopters and distinctively marked. No adopters abandoned their adopted nests during the observation period. Adopting females were observed to consume eggs and young larvae, provision older larvae, and oviposit on the adopted nest.

The enclosure population number was determined by summing the number of foundresses that initiated colonies ($n=57$), the number of adopting queens ($n=35$) and the number of wasps not associated with any nest. The latter was determined using the Petersen method of capture–recapture (Krebs 1972). On 29 June 1996, 30 wasps out of an unknown enclosure population size (x) were net-captured at a common feeding site, distinctly marked with Testors enamel paint, and released. On 3 July 1996, the same techniques were used to capture a second sample of 30 wasps. Fourteen of these wasps had been marked during the first capture–release event. Thus, the unknown population contained *ca.* 65 wasps [$30/x=14/30$ and x *ca.* 65].

3. RESULTS

The total wasp population size was approximately 157. Fifty-seven wasps initiated colonies and 100 wasps were not associated with any colony before the adoption experiment. Thirty-five wasps secured 29 of the 35

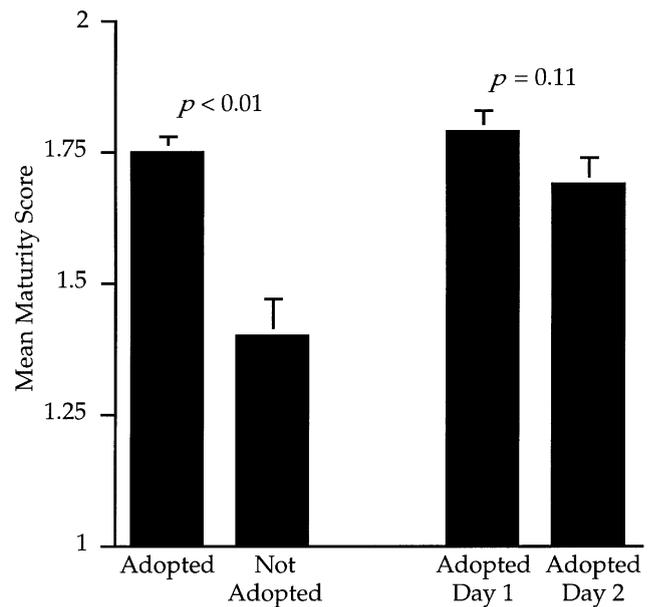


Figure 1. Mean maturity score of colonies adopted, not adopted, adopted day 1 and adopted day 2. Columns represent means and error bars represent standard errors.

queenless nests (six of the nests were co-adopted). The remaining unadopted nests ($n=6$) were cannibalized. Adopters ($n=35$) were exclusively from the population of wasps not previously associated with a colony, and thus had not been subordinates on multiple-foundress colonies (chi-squared test: $\chi_1^2=5.23$, $p<0.03$). This result shows that adopters did not initiate colonies before adopting an abandoned nest.

Adopted nests were significantly more mature than unadopted nests (Mann–Whitney *U*-test: $n_1=29$, $n_2=6$, $p<0.01$; figure 1). Nests adopted on day 1, however, were not more mature than those adopted on day 2 ($n_1=15$, $n_2=14$, $p=0.11$; figure 1). Although more mature, adopted nests were not significantly larger than unadopted nests (table 1). These results indicate that individuals engaging in the 'sit-and-wait' strategy preferentially adopt the most mature nests.

Adopted nests had significantly more fourth and fifth instar larvae than nests that were not adopted (table 1), and nests adopted on day 1 had significantly more fourth and fifth instar larvae than nests adopted on day 2 (table 1). There was no significant difference between adopted and unadopted nests or between nests adopted on day 1 and nests adopted on day 2 with respect to the number of cells, eggs, first, second and third instar larvae, or pupae (table 1).

4. DISCUSSION

These data confirm that a subset of spring females of *Polistes dominulus* do not initiate colonies but rather wait to adopt (or possibly usurp) colonies initiated by other conspecifics. These results are the first to document conclusively this alternative reproductive strategy in paper wasps, and thus confirm the proposal of Nonacs & Reeve (1993, 1995).

Individuals performing this reproductive strategy may be (i) rescuing non-descendant kin, (ii) subordinate

Table 1. Characteristics of adopted nests

number	adopted (<i>n</i> =29)	not adopted (<i>n</i> =6)	adopted versus not adopted ^a	adopted day 1 (<i>n</i> =15)	adopted day 2 (<i>n</i> =14)	adopted day 1 versus day 2 ^a
pupae	6.72±0.72	4.17±1.42	<i>p</i> =0.173	7.20±0.93	6.21±1.13	<i>p</i> =0.456
4 & 5 instar larvae	7.07±0.83	1.67±0.47	<i>p</i> =0.003	9.00±1.27	5.00±0.76	<i>p</i> =0.023
1, 2 & 3 instar larvae	6.00±0.56	5.17±1.05	<i>p</i> =0.537	6.27±0.86	5.70±0.72	<i>p</i> =0.553
eggs	28.93±1.53	22.67±4.86	<i>p</i> =0.154	30.47±2.55	27.29±1.59	<i>p</i> =0.484
cells	48.38±2.46	36.50±7.14	<i>p</i> =0.161	52.27±4.04	44.21±2.35	<i>p</i> =0.156

^a All tests are Mann–Whitney tests. All results are presented as mean±standard errors. Cell number is an indicator of overall nest size.

foundresses leaving a multi-foundress association, (iii) foundresses whose nest has been damaged or destroyed, (iv) physiologically constrained (Gadagkar 1991; but see Nonacs & Reeve 1993, 1995), or (v) maximizing direct fitness benefits (Nonacs & Reeve 1993, 1995). Females were not rescuing non-descendant kin in this study because nests were gathered from sites so distant that the possibility of kinship with an adopter was highly unlikely. In addition, possibly owing to competition from the large number of females not associated with a nest, the adopting females were not subordinate foundresses nor, owing to the experimental design, were the adopters foundresses whose nests had been destroyed. It appears, as has been suggested from field observations (Nonacs & Reeve 1993), that the adopters within the enclosure were maximizing selfish interests by selecting nests to adopt based on colony maturity (figure 1).

Whether the adopters were physiologically constrained, causing a delay in reproductive capabilities (Gadagkar 1991), and making the best of a bad situation or were unconstrained and facultatively delaying reproduction cannot be discerned from this data set. Regardless, individuals who sit and wait are choosing nests to adopt that are most likely to survive to reach the worker phase, when the probability of colony survival greatly increases (Reeve 1991; Nonacs & Reeve 1993).

Colony death due to the loss of a foundress prior to worker emergence is common and has been shown to be a risk sufficient to render multiple-foundress associations beneficial (i.e. the survivorship insurance model (Reeve 1991; Nonacs & Reeve 1995; Reeve & Nonacs 1997)). Preferentially adopting mature nests may be an alternative mechanism to ensure individual possession of a colony that reaches the worker phase. Thus, this study suggests that individuals may delay nest building and 'sit and wait' for the opportunity to adopt an orphaned colony as an alternative to founding a colony singly or cooperating in early-season, multiple-foundress associations.

Finally, since pupae will eclose as adults the earliest, it is surprising that pupae number did not significantly differ between adopted and unadopted nests. Instead, the number of fourth and fifth instar larvae was the best predictor of nest attractiveness. Although not addressed in this study, at least two non-mutually exclusive hypotheses could explain the attractiveness of nests abundant in

late-instar larvae, both of which would lead to more unrelated workers remaining rather than abandoning the nest: (i) the effective cue scrambling and (ii) the indirect fitness inducement-to-remain hypotheses. The cue scrambling hypothesis suggests that larvae exposed through interactions to the adopting foundress's cues are more likely to remain and work on the nest than individuals not exposed to the foundress's cues (i.e. pupae, owing to the pupal cap). The inducement hypothesis suggests that workers unrelated to the adopter are more likely to remain on the nest if a large proportion of late-instar larvae, related to the worker, would benefit from the presence of the worker and obtain some direct reproduction as a result. Both hypotheses may explain why adopting foundresses, although still selecting the most mature nests, preferentially select nests with a large number of late-instar larvae.

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