Dedicated to the memory of William Donald Hamilton

Alternative reproductive tactics in the paper wasp *Polistes dominulus* with specific focus on the sit-and-wait tactic

Philip T. Starks

Division of Insect Biology, University of California at Berkeley, Berkeley, CA 94720-3112, USA (e-mail: starks_p@uclink.berkeley.edu)

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Polistes dominulus females that adopt nests are less cooperative and may expend less energy than nest founding wasps. In an enclosure, 14 nests were adopted by individuals previously unassociated with any nest. No preference for enclosure or non-enclosure nests was detected, suggesting that adopters do not preferentially secure nests containing non-descendent kin. Instead, adopters — who were significantly less likely cooperate than nest constructing wasps — maximized direct fitness benefits by adopting nests most likely to produce reproductives. Preliminary data comparing body weights of adopters to nest constructors suggests that, relative to nest constructors, adopters gain weight during the nest founding period. Combined, these results indicate that adopters are less cooperative than nest initiators, prefer mature nests to nests with a higher likelihood of kinship, and may conserve energy during the nest founding period. Several additional reproductive tactics were observed and a preliminary flow diagram of these options is provided.

"Social wasps are among the least loved insects. … Yet, where statistics will not alter a general impression, another approach might. Every schoolchild, perhaps as part of religious training, ought to sit watching a *Polistes* wasp nest for just one hour. … I think that few will be unaffected by what they see. It is a world human in its seeming motivations and activities far beyond all that seems reasonable to expect from an insect: constructive activity, duty, rebellion, mother care, violence, cheating, cowardice, unity in the face of threat — all these are there."
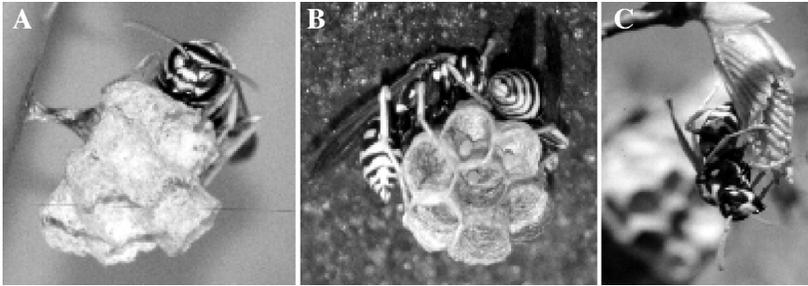
W. D. Hamilton (1996)

Fig. 1. — **A**: a single foundress nest. — **B**: a multiple foundress nest. — **C**: a potential sit-and-wait wasp. Photos courtesy of C. A. Blackie (photos **A** and **B**) and J. Shellman-Reeve (photo **C**).

Introduction

W. D. Hamilton was no doubt fascinated by the diversity of behavior observed on *Polistes* nests (*see* Turillazzi & West-Eberhard 1996). Indeed, this diversity is apparent even before a single egg is laid. During the colony initiation period, *Polistes* foundresses display several different forms of nest founding behavior (*see* Reeve 1991, Turillazzi & West-Eberhard 1996). Spring foundresses sometimes initiate colonies alone (Fig. 1A), form associations with other females (Fig. 1B), usurp established conspecific colonies, or even adopt abandoned nests (Fig. 1C). Females that adopt abandoned nests may have left multiple-foundress associations (Nonacs & Reeve 1993), lost their colonies due to predation or other forms of damage (Cervo & Dani 1996), or waited to adopt an orphaned nest instead of initiating one of their own (Nonacs & Reeve 1993, Starks 1998). Within an enclosure, Starks (1998) showed that the *P. dominulus* females who engage in the sit-and-wait reproductive tactic preferentially adopt the most mature nests (*see also* Nonacs & Reeve 1993) and show a preference for orphaned nests with a large number of fourth and fifth instar larvae. As with cases of usurpation (Klahn 1988), once adoption had occurred, adopters destroyed the previous foundress' eggs and early instar larvae and replaced them with their own eggs; the older larvae and pupae were allowed to complete development (Starks 1998).

Wasps that perform the sit-and-wait tactic — those that do not engage in nest construction but rather adopt orphaned nests — may be rescuing non-descendant kin (i.e., reaping kin selective benefits; Hamilton 1963, 1964a, 1964b), maximizing direct fitness benefits (Nonacs & Reeve 1993, 1995) or physiologically constrained from initiating nests (Gadagkar 1991). In the previous enclosure experiment (Starks 1998), all sit-and-wait wasps were from a population of wasps who did not engage in nest founding behavior prior to the adoption experiment. Since the nests made available for adoption were gathered from locations geographically distant from the natal territory of the enclosure wasps, the sit-and-wait wasps were not rescuing non-descendant kin. However, the possibility that these wasps were physiologically constrained from initiating their own nests could not be ruled out nor could the hypothesis that these wasps would *preferentially* adopt nests containing non-descendant kin because all adoptable nests contained unrelated larvae.

In an attempt to address these questions, an additional enclosure experiment was conducted. To address the possibility that sit-and-wait wasps preferentially adopt nests containing related larvae, both enclosure and non-enclosure nests were made available for adoption. To address the possibility that the sit-and-wait wasps were physiologically constrained from initiating nests, overwinter weights were gathered on all captive wasps. Gadagkar and colleagues (1991) showed in *Ropalidia marginata* that wasps fed relatively well as larvae had a higher probability of constructing nests and a shorter period required to obtain reproductive maturation. Accordingly, lighter *P. dominulus* wasps may be less likely to engage in nest construction than heavier wasps. As a result of this experiment, characteristics relating to spring female behavior was gathered.

Methods

Enclosure population

During the winter of 1996–1997, gynes (future queens) from colonies that successfully completed an entire colony cycle within a wooden-frame screen enclosure ($4.88 \times 3.66 \times 2.14$ m) at Cornell University's Liddell Field Station over-wintered. All wasps ($n = 148$) within the enclosure were located during the winter, weighed on a field scale (to 0.001 grams), and given individual marks with Testor's enamel model paint. After foundresses broke hibernation in early May, wasps were provisioned with water, honey-water, and chopped mealworms and crickets. The enclosure contained a wide variety of wildflowers and a constant running water source. All nests were easily located and the enclosure was censused daily.

Characteristics of adoptable nests

On 22 June, 10 pre-worker phase single foundress *P. dominulus* nests, collected from two sites in the Ithaca area, were attached to empty nestboxes with wood-glue and a pin anchor. Colonies were collected from sites distant from the natal territory of the enclosure wasps (*see* Starks 1998). An additional 12 single foundress nests from within the enclosure were selected for the adoption experiment. Foundresses from these colonies were collected at night, weighed, and removed from the enclosure; their nests were taken down and reattached in the same nestbox employing the procedure used on nests collected from outside the enclosure. All adoptable nests were similar in size and development and were available for adoption prior to wasp activity on the morning of 23 June.

All queens were removed from the 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: first, second, and third instar larvae or fourth and fifth instar larvae. Based on developmental periods (Pardi 1951, Strassmann & Orgren 1983) an overall nest maturity score was calculated for each nest (*see* Starks 1998). These nests were censused daily until all adoptions ceased.

Identification of adopting wasps

Identification of adopters was performed as in Starks (1998): individuals who remained on and defended a nest made available for adoption were identified as adopters. Adopters were identified, removed from the adopted nest during the late evening, weighed on the field scale, and immediately returned to their new nest. All adopters remained on their adopted nests during the observation period. These females were observed to consume eggs and young larvae, as well as perform normal foundress behavior (i.e., provision older larvae and oviposit on the nest).

Temperature data

Temperature data was gathered from the north, south, east and west walls of the enclosure twice daily (approximately 1000 and 1600 hours). Temperature differentials were expected due to the presence of a cooling system on the southern wall of the greenhouse, approximately 1.25 m outside of the wooden enclosure.

Statistical methods

Weight data were analyzed with Student's *t*-tests, temperature data with paired *t*-tests, and behavioral data with χ^2-tests when appropriate. Wasps were assigned to one of three categories (single foundress, multiple foundress, or sit-and-wait wasp) on the basis of its behavior. Wasps that performed no reproductive behavior (i.e., those that died prior to helping in the construction of a nest or prior to laying any eggs) were excluded from the analysis. All data were analyzed with the statistical package DataDesk 6.1 (Velleman 1998).
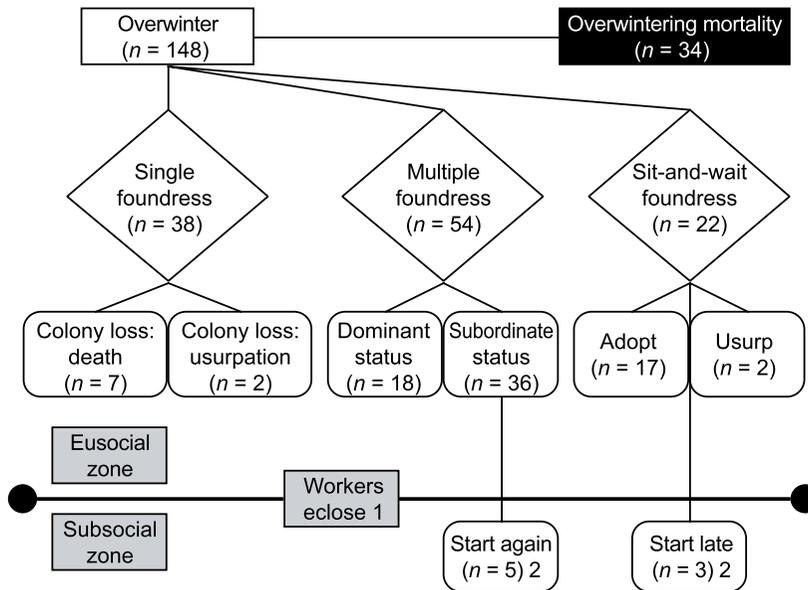
Fig. 2. Schematic of reproductive options available to *Polistes dominulus*. All wasps overwintered and in the spring each individual either initiated a colony (as a single foundress or in an association with another foundress) or did not initiate a colony. *N*-values represent the number of observations that a particular option was observed. Eusocial zone and subsocial zone represent characteristics of colonies produced during different periods of a single field season. Since late colonies will not have workers, no cooperative care of young will occur and thus the colony is not eusocial. — 1: After workers eclose, adoptions and usurpations are no longer possible due to active worker colony defense. — 2: Due to time restrictions, colonies initiated during the population's worker phase are likely to produce only reproductives.

Results

### General population characteristics

Enclosure population

The total overwintering wasp population size was 148. Between 17 May and 15 June, 92 wasps initiated colonies while the remaining wasps did not associate with any colony. Of the 92 nest-initiating wasps, 38 constructed nests alone and the remaining 54 cooperated in the initiation of 18 nests (Fig. 2). This multiple-founding frequency closely resembles the frequencies observed in natural populations within the Ithaca area (P. T. Starks, unpubl. data) and in the previous enclosure experiment (Starks 1998). No difference in overwintering weight was detected between the three categories of wasps (in grams ± SE: total population, 0.090 ± 0.016; single foundresses, 0.093 ± 0.019; multiple foundresses, 0.090 ± 0.014, individuals unasso-

ciated with any colony, 0.089 ± 0.017; *t*-test, *p* > 0.30 for each comparison). Foundress behavior appeared normal: wasps foraged, oviposited and fed larvae. Thirty-four wasps (~23%) did not survive to engage in nest initiation or reproductive behavior.

Single foundress colonies

Twelve single foundresses were removed from their nests in order to provide sit-and-wait wasps the opportunity to adopt enclosure nest. Seven of the remaining 26 single foundress colonies failed due to the death of the foundress. Of the remaining 19, the original foundresses lost two colonies to successful usurpation events. These usurpation events lead to the death of the original foundress and were performed by wasps unassociated with any nest (Fig. 2). Thus, the probability that a lone foundress would survive to produce workers within this relatively safe

Maturity score

Fig. 3. — **A**: Mean maturity score of adoptable colonies from within the enclosure ('Naturally founded') and of adoptable colonies from the natural Ithaca NY population ('Transplanted'). — **B**: Mean maturity score of colonies adopted and of colonies non-adopted. Columns represent means and error bars represent standard errors.
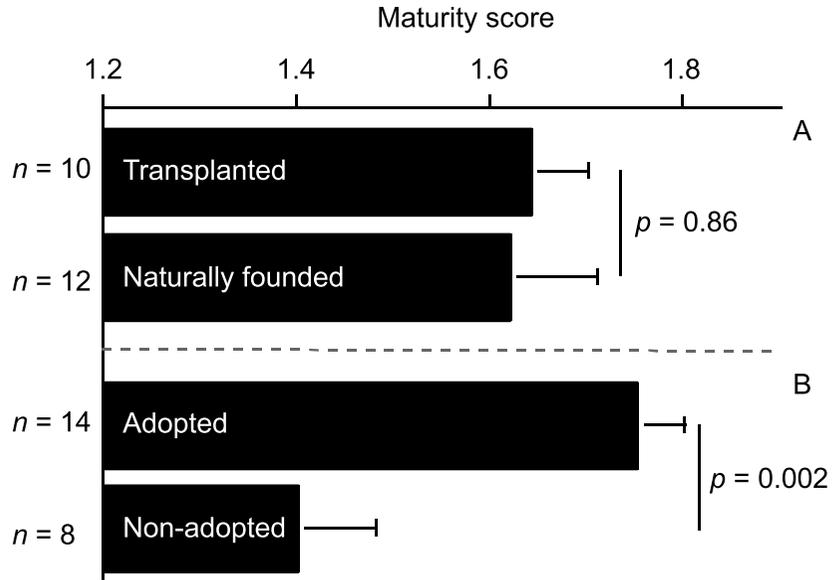
environment was ~76%. (This statistic assumes that all foundresses removed for the experiment would have survived and thus represents the highest possible success rate.)

Multiple foundress colonies

All multiple foundress colonies ($n = 18$) survived to produce workers (100% success rate). After the production of workers, subordinate foundresses ($n = 34$) on 16 of the 18 multiple foundress colonies no longer associated with the colony. Five of these subordinate foundresses were later observed to initiate new single foundress nests during the worker phase of their original colony (Fig. 2). Interestingly, as has been documented in *P. fuscatus* (Reeve *et al.* 1998), four subordinate foundresses were among the first workers on colonies from the previous season. None of these individuals, however, survived to see workers eclose (emerge) on the colonies they helped build.

Sit-and-wait foundresses

Seventeen wasps secured 14 of the 22 adoptable nests (3 nests were co-adopted). All remaining abandoned nests were cannibalized. As with Starks (1998), adopters were exclusively from the population of wasps not previously associated with a colony, and thus had not been subordinates on multiple-foundress colonies or individuals whose nests had been damaged or destroyed. Two sit-and-wait wasps usurped colonies from single foundresses and three initiated colonies during the worker phase of the population (Fig. 2).

Characteristics of adopters

Nest preference

Nests made available from within the closure ('naturally founded') did not differ in maturity from those transplanted into the enclosure from the surrounding Ithaca area (Fig. 3A), nor was there a preference for either transplanted or naturally founded nests ($\chi^2 = 2.98$, $p = $ ns). Adopted nests, however, were significantly more mature than non-adopted nests (Fig. 3B). These results indicate that individuals engaging in the sit-and-wait tactic preferentially adopt the most mature nests. Although more mature, adopted nests were not significantly larger than non-adopted nests. As with Starks (1998), the characteristic that best distinguished adopted from non-adopted nests was the number of 4th and

5th instar larvae: adopted nests had significantly more larvae of this stage than did non-adopted nests (Table 1).

Cooperation

Of the 22 sit-and-wait wasps (n = 17 adopters, n = 2 usurpers, n = 3 late nest constructors), only six individuals cooperated with other foundresses. This proportion of cooperation within these wasps (~27%) was significantly lower than with early season nest constructing wasps (~59%; χ^2 = 13.27, p < 0.001; Fig. 4). These data suggest that sit-and-wait wasps are less likely to engage in cooperative associations than are typical foundresses.

Weight

Although overwintering weight did not differ (t = 0.414, p = 0.68), a comparison of the change in weight from overwintering until the time of colony adoption showed that sit-and-wait wasps (n = 17) gained weight during the nest founding period whereas wasps (n = 12) engaged in nest construction, nest defense and larvae provisioning lost weight, albeit a very small amount (t = 2.21, p < 0.04; Fig. 5). These data raise the possibility that adopters conserve energy during the nest-founding period. These weight change data should be viewed cautiously: since the values were very small they could possibly reflect random factors such as recent food consumption or differences in paint mark weights. (Weight measures were taken during the evening long after foraging had ceased to minimize the former problem.) For these, and similar reasons,

a more fine-scale analysis of weight differences was not undertaken.

Sit-and-wait wasps often perched in large groups on the southern wall of the enclosure during periods of the day and during the night. The southern wall was significantly cooler than any other wall within the enclosure (S: 26.14 ± 0.71 °C; N: 29.47 ± 0.94 °C; E: 26.96 ± 0.84 °C; W: 27.12 ± 0.74 °C; S vs. E, paired *t*-test, t_{112} = 7.420, p < 0.0001). Similar aggregations were not observed on the other three walls of the enclosure. This result suggests that, in addition to not constructing nests, defending nests or provisioning larvae, sit-and-wait wasps may conserve energy by preferentially perching in relatively cool locations.

Discussion

Results presented here suggest that that sit-and-wait wasps are less cooperative on average than wasps that initiate colonies, prefer mature nests over ones with a higher likelihood of kinship, and may conserve energy during the nest founding period. These results suggest that the sit-and-wait wasps are not preferentially rescuing non-descendent kin, nor do they appear to be physiologically constrained from initiating a colony. Instead, it appears that nest adoption is a mechanism to maximize the probability of possessing a mature pre-worker phase colony without expanding excessive energy during the nest founding period or cooperating in the construction of the nest.

Observations of reproductive behavior within the enclosed population demonstrate that there are multiple reproductive options available to *Polistes dominulus*. Because individuals ap-

Table 1. Characteristics of adoptable nests.

	Adopted (n = 14)	Non-adopted (n = 8)	Adopted vs. Non-adopted*
Pupae	5.20 ± 1.30	2.50 ± 1.13	p = 0.131
4 and 5 instar larvae	6.36 ± 0.49	2.25 ± 0.96	p = 0.003
Eggs and 1, 2 and 3 instar larvae	29.71 ± 3.88	32.25 ± 4.62	p = 0.680
Cells	41.29 ± 5.06	37.00 ± 6.01	p = 0.593

* All tests are Student's *t*-tests. All results are presented as mean ± SE. Cell number is an indicator of overall nest size.
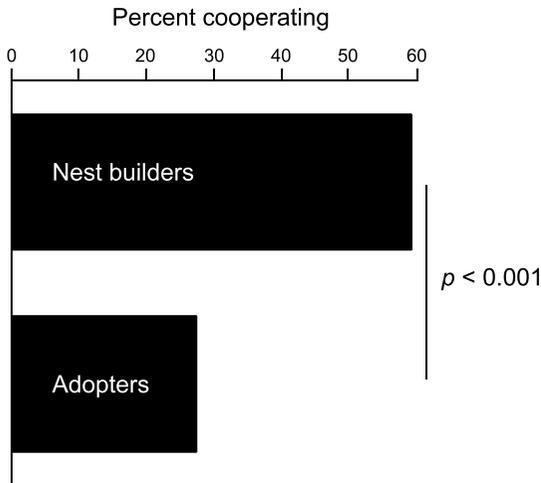
Percent cooperating

Fig. 4. Percent of colonies containing multiple foundresses. 'Nest builders' represents the population of wasps who initiated colonies (i.e. engaged in nest construction) and 'Adopters' represents the population of wasps that did not initiate nests but rather waited for the opportunity to adopt an adoptable (i.e. abandoned) colony. Columns represent percents.

Mean weight change (g)

Fig. 5. Mean weight change between overwintering weight and weight at the time of the adoption experiment for wasps who engaged in nest construction ('Nest builders') and those who adopted orphaned nests ('Adopters'). Columns represent means and error bars represent standard errors.

peared able to select from a suite of options (Fig. 2), it is likely that each option is a tactic in a single reproductive strategy. I will first discuss the selective maintenance of alternative phenotypes in a population and then discuss the specifics of *P. dominulus's* reproductive behavior.

Alternative reproductive behaviors

Following Dominey (1984) and Austad (1984), Gross (1996) provided a framework for understanding the selective maintenance of alternative behavioral phenotypes. Using mating behavior as an example, Gross described genetic polymorphisms, mixed evolutionary strategies, and conditional strategies. If a population of individuals display multiple tactics and each tactic is specific to a single strategy, the population is genetically polymorphic for the given behavior. As such, each individual performs only one tactic regardless of context. To be maintained in a population, the set of tactics must have negatively frequency dependent fitnesses that equalize at an intermediate fre-
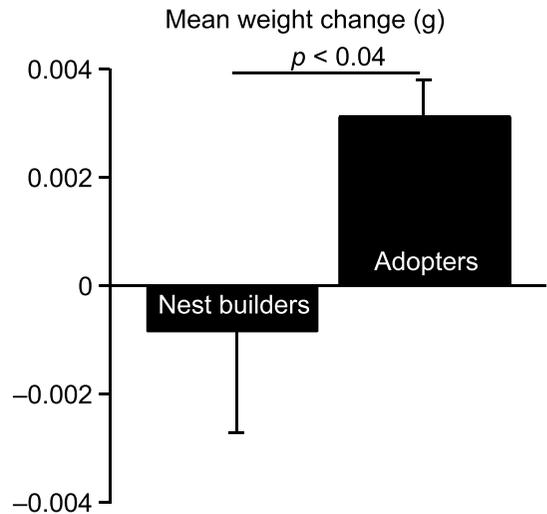
quency.

Mixed evolutionary strategies (ESS) and conditional strategies, on the other hand, are not underlain by genetic differences between individuals — all tactics arise from a single genetic strategy (Gross 1996). The characteristics that most clearly distinguish between these two kinds of strategies are the probabilities of expression and fitness payoff of each tactic. A population engaged in a mixed ESS, defined by two tactics, contains multiple individuals performing tactic 1 with a probability (p) and tactic 2 with a probability ($1 - p$). As with genetic polymorphisms, tactics in a mixed ESS must have negatively frequency dependent fitnesses and equal average fitness payoffs to be selectively maintained in a population (Maynard Smith 1982).

Conditional strategies, however, are characterized by individuals adopting the tactic that has the highest payoff for the individual's given condition (Gross 1996). Condition-based alternative phenotypes are expected to have a switchpoint where the fitness payoff for either tactic is identical. At conditions above or below the switchpoint, individuals are expected to display

the phenotype that has the highest average fitness payoff. Gross (1996) suggested, and a recent review by Kain (1999) supports, that alternative reproductive phenotypes (i.e. mate acquisition) are likely to be different tactics in a conditional strategy for most insect populations.

Since some *P. dominulus* individuals expressed multiple behaviors within their lifetime (e.g., the sit-and-wait wasps and subordinates from multiple foundress associations who constructed late season nests), it does not appear that reproductive behavior in *P. dominulus* results from a genetic polymorphism. Because reproductive behavior in *P. dominulus* does not appear to be underlain by genetic differences, reproductive behavior is likely to be best described by a genetically monomorphic model where multiple potential options (tactics) are available to each foundress.

Due to the lack of reproductive fitness data, discerning between the models based on the assumption of genetic monomorphism (mixed ESS or conditional strategy) is not possible from this data set. It is possible, however, that reproductive behavior in *P. dominulus* females is influenced by the level or quality of nutrition received as a larva (*see* Gadagkar *et al*. 1988, O'Donnell 1998). Thus, although no weight difference was detected between nest initiating and sit-and-wait wasps, the quality of larval nutrition could set the conditions that influence future reproductive behavior. Such influences in a conditional strategy would be transparent to the methods employed in this project.

The sit-and-wait reproductive tactic

Individuals performing the sit-and-wait reproductive tactic may be rescuing non-descendant kin, physiologically constrained, or maximizing direct fitness benefits. In this study, females were given the opportunity to adopt nests with an increased likelihood of containing kin (i.e., those from the same small population) but instead selected the most mature nest regardless of the site of origin. The interpretation that these wasps were not preferentially adopting kin rests on the reasonable assumption that individuals will be more likely to share a degree of relatedness with nests from their own small population than with nests gathered from distant populations. Naturally, a fine-scale examination of this question would include genetic analysis. However, since *P. dominulus* recognition behavior can be influenced by environmental cues (Picket *et al*. 2000) and since kin discrimination is heightened in contexts suggesting a fitness payoff (Starks *et al*. 1998), the sit-and-wait wasps should have preferentially adopted nest containing similar environmental cues (i.e., enclosure nests) if they wanted to maximize their chances of rescuing non-descendent kin. Thus it does not appear that rescuing non-descendant kin is prioritized over the quality of an adoptable nest.

Sit-and-wait wasps may be physiologically constrained from initiating nests. The overwintering weight of foundresses was not predictive of reproductive tactic, however, as might be expected from Gadagkar (1991). Relative to nest constructing individuals, adopters gained weight during the nest founding period (Fig. 5). This increase in weight was most likely due to two factors: first, adopters did not perform any of the energetically costly behaviors associated with nest ownership (e.g., cell construction, foraging, nest defense, etc.) and second, adopters congregated in the coolest part of the enclosure. Interestingly, although adopters were less cooperative than nest founding wasps (Fig. 4), these individuals often congregated in large groups. Perhaps these associations are mutually beneficial in that they may decrease the possibility of being preyed upon (i.e., there may be safety in numbers).

These weight data, combined with the observations that some sit-and-wait wasps eventually constructed nests and that adopters oviposited shortly after securing colonies, suggest that these animals are not physiologically constrained from nest initiation. The physiological constraint hypothesis, however, cannot be entirely ruled out. Although it is clear that these animals can initiate nests, it is not clear whether ovarian development in these animals is delayed. Delays in reproductive maturation may have profound impact on reproductive behavior (Gadagkar 1991).

The final hypothesis — that sit-and-wait wasps are maximizing direct fitness benefits — is best supported by the data. Given a range of nests to choose from, the sit-and-wait wasps preferentially adopted the most mature nests. Since more mature nests will produce workers sooner than less mature nests, and since nests with workers are more likely to survive than those without, the sit-and-wait wasps seem to be maximizing direct fitness benefits. Accordingly, it appears that nest adoption is a mechanism to maximize the probability of possessing a mature pre-worker phase colony without expanding excessive energy during the nest founding period or cooperating in the construction of the nest.

It is important to note that the previously stated hypotheses for the expression of the sit-and-wait tactic are not mutually exclusive. It is quite likely that there are multiple paths to the performance of the sit-and-wait reproductive tactic. Indeed, providing that founding options are not controlled by a genetic polymorphism, the more interesting question is what conditions lead the adoption of the sit-and-wait tactic. Clearly any complete answer of this question will incorporate a frequency dependant component: since colonies with multiple foundresses rarely fail (Reeve 1991, *see also* Results), the success of the sit-and-wait tactic will be inversely proportional to the frequency of multiple foundress colonies in the population.

Early "workers" and other subordinate foundresses

Data presented here also support Gadagkar's (1991) hypothesis that relative condition may lead to the expression of a helper (i.e., subordinate) tactic. All four foundresses who were originally early eclosing workers during the previous field season became subordinate foundresses within multiple foundress associations. As these animals were much older than the other foundresses, it is perhaps not surprising that none of these individuals survived to see workers eclose on their nests. Providing that they received some reproduction or that they joined a related dominant foundress, these individuals

reaped a fitness payoff for their pre-worker phase efforts. This payoff was likely to be small, however, which draws into question the inclusion of early workers as the primary reproductive payoff for subordinate foundresses in transactional skew models (e.g., Reeve *et al*. 2000).

Several subordinate foundresses ($n = 5$) constructed new nests after their association with the dominant foundress was terminated. These new nests, initiated relatively late in the season, would produce only reproductive destined individuals (i.e., gynes and males). Exploiting this subsocial tactic may be a mechanism for reaping additional lifetime reproductive fitness. This tactic, however, is likely to pose great risks. Assuming that competition exists between wasps for foraged items, these previously subordinate foundresses would now be competing against a large worker wasp population. At a minimum, this increased competition would necessitate longer foraging trips, which would increase susceptibility of the new nest to intra-specific (cannibalism) and inter-specific predation.

Dominate foundresses

Dominant foundresses faired well during this observation period: all but two were in sole possession of a colony during the period when reproductives are produced and the remaining two each shared custody with only one other female. In this study, the probability that a multiple queen colony would survive to produce workers was 100% whereas the probability that a single foundress colony would fair as well was, at best, only 76%. This difference in survival probability may influence some individuals to adopt colonies rather than construct their own, i.e., preferentially adopting mature nests may be a mechanism to ensure possession of a colony that reaches the worker phase (Starks 1998). Indeed, colony death due to the loss of a foundress prior to worker emergence is common (*see* Results) and has been shown to be a risk sufficient to render multiple-foundress associations beneficial (Reeve 1991, Nonacs & Reeve 1995, Reeve & Nonacs 1997).

Unnatural conditions?

The diversity of behavior observed within the enclosure was very rich (Fig. 2). It is possible that the frequency of some of these behaviors was enhanced due to the environmental conditions (*see* O'Donnell 1998). Certainly, wasps did not experience large-scale (e.g. bird) or small-scale (e.g. spider) predation, both of which are common in the Ithaca area (author's pers. obs.). However, it would be premature to suggest that these behaviors were *caused* by the environmental conditions, i.e., that the expression occurs only in unnatural situations. There are three lines of evidence that argue against such a pessimistic view: previous field studies have documented adoption in *P. dominulus* (Nonacs & Reeve 1993), the frequency of multiple foundress colonies within the enclosure was similar to natural populations (*see also* Starks 1998), and the maturity scores of nests did not differ based on whether or not they were enclosure colonies (Fig. 3). Rather than an unnatural response to captivity, these behaviors may be representative of the suite — or even a subset — of behaviors available to *P. dominulus*. Due to the difficulty of locating cryptic nests within the field and the possibility of individuals emigrating from a given field site, enclosure studies may offer the best opportunity to examine alternative reproductive tactics in *Polistes* wasps.

Conclusion

Results presented here suggest that that sit-and-wait wasps conserve energy during the nest founding period, that they prefer mature nests over ones with a higher likelihood of kinship, and that they are less cooperative on average than wasps that initiate colonies. These results suggest that the sit-and-wait wasps are not preferentially rescuing non-descendent kin nor do they seem to be physiologically constrained from initiating a colony. In addition, observations of reproductive behavior within the enclosed population demonstrates that there are multiple reproductive options available to *P. dominulus*. Because individuals appeared able to select from a suite of options, it is likely that each option is a tactic in a single reproductive strategy (i.e., is not underlain by a genetic polymorphism).

Interestingly, a few individuals (subordinate foundresses and sit-and-wait wasps) constructed nests late in the season and thus did not benefit from the help of worker wasps, i.e., they attempted to produce a single reproductive brood. This apparent subsocial behavior may be an additional mechanism for increasing lifetime reproductive fitness and accordingly may be suitable for inclusion in models of reproductive skew that incorporate life history components.

Finally, the quote opening this paper suggests that W. D. Hamilton would have loved the sit-and-wait wasps. He might have considered these animals lazy since they do not construct nests, cooperative only when it suited them (in hiding but not in tending nests), deceitful by usurping the efforts of unrelated workers, and honest in their attempt to maximize direct fitness. Although referring to a mature colony when he wrote it, Hamilton's quote is equally appropriate for this small subset of wasps, "[i]t is a world human in its seeming motivations and activities far beyond all that seems reasonable to expect from an insect" (1996).

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