

UCLA

UCLA Previously Published Works

Title

Opportunistic adoption of orphaned nests in paper wasps as an alternative reproductive strategy

Permalink

<https://escholarship.org/uc/item/3qr1r4vz>

Journal

Behavioural Processes, 30(1)

ISSN

0376-6357

Authors

Nonacs, Peter

Reeve, Hudson K

Publication Date

1993-08-01

DOI

10.1016/0376-6357(93)90011-f

Copyright Information

This work is made available under the terms of a Creative Commons Attribution License, available at <https://creativecommons.org/licenses/by/4.0/>

Peer reviewed

BEPROC 00482

Opportunistic adoption of orphaned nests in paper wasps as an alternative reproductive strategy *

Peter Nonacs and Hudson K. Reeve

Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, USA

(Accepted 25 January 1993)

Abstract

Adoption of abandoned or orphaned nests by adult females occurs commonly during the colony-founding period of the primitively eusocial paper wasp, *Polistes dominulus*. Our evidence indicates that adoption reflects: (1) 'making the best of a bad situation,' for queens who have lost their nests; (2) subordinates leaving multiple-foundress associations; and (3) possibly, a 'sit-and-wait' strategy, in which non-nesting females wait for nests to be orphaned. A 'sit-and-wait strategy' implies that wasps facultatively delay personal reproduction rather than that the delay in reproduction is due to physiological constraints (sensu Gadagkar, 1991a). Orphaned nests with related brood are not more attractive than those bearing unrelated brood, suggesting that nest-adoption has not evolved primarily as a strategy to rescue non-descendant kin. Instead, all wasps tend to adopt nests that theoretically maximize their selfish genetic interests: the most attractive nests were large combs at an advanced stage of development. These nests can produce more workers and are closer to worker emergence, at which time colony survival per unit time dramatically rises. The primary proximate cue for adoption seems to be whether nests contain later-instar larvae or pupae. Since developmental stage of brood correlates with nest size, preferred nests thus tend to be relatively mature and large.

Key words: Adoption; Alloparental care; Alternative reproductive strategy; Colony founding; *Polistes dominulus*; Wasp

Correspondence to: P. Nonacs, (Present address) Center for Population Biology, University of California, Davis, CA 95616, USA.

* This paper was presented at the Workshop on Parental Investment, University of Lausanne, Switzerland, in July 1992.

Introduction

Adoption of orphaned offspring is common in vertebrates like mammals and birds that have well-developed and energetically expensive parental care (Riedman, 1982; Pierotti, 1991). In some cases, adoption or alloparental care is clearly adaptive because the adopter and adoptee are likely to be close kin. In cases where relatedness between the two parties is negligible, adoption has been suggested to be either pathological (Riedman, 1982) or intergenerational conflict won by offspring (dependent young successfully parasitizing unrelated adults: Pierotti, 1991). Nonacs (1991), however, derived a model of alloparental care where adoption is favored, even when the relatedness of the care-giver and the orphan is quite low, as long as the care-giver's future reproductive success or options are limited and if the care given to the orphan is likely to greatly increase the orphan's survivorship. This model was a modification of Queller's (1989) model of the evolution of eusociality in the Hymenoptera. Queller proposed that the combination of highly dependent young and low success rate of independent-founding favors daughters remaining with their natal nest and hence the evolution of multi-generational cooperative societies (i.e. eusociality).

In such discussions about the evolution of eusociality, attention almost inevitably turns toward wasps and, in particular, toward the paper wasps (Polistinae), because of their perceived intermediate position in the evolution of eusociality (Evans, 1958; Wilson, 1971; Gadagkar, 1991a,b; Reeve, 1991). Although these species form societies with multiple, overlapping generations, individual wasps are not obligately bound into either worker or reproductive (queen) castes. As far as is known, all primitively eusocial wasps retain the ability to both mate and raise offspring on their own. It is the variation in both what a wasp can do and what a wasp does do in regard to the raising of young that makes them attractive candidates for the study of parental strategies and investment.

Temperate *Polistes* species are all annual in that colonies are started in the spring, grow throughout summer, and produce new sexuals in the fall. Except for the mated female sexuals, all wasps die before winter (review in Reeve, 1991). The sexuals that start the colonies in the spring (the foundresses) have several options. First, they can nest alone, constructing the comb and raising the first brood without assistance from any other individual. Second, they can nest together in groups of from two to tens of females, depending on the species. Within such groups strict dominance hierarchies typically form, and generally only the most dominant individuals will contribute the majority of eggs. However, at any time individuals from within the group or from outside of the group may attempt to replace or usurp the dominant. Many usurpers come from other nests (Gamboa, 1978; Klahn, 1981, 1988), but others may simply be 'waiting in the bushes' for an opportune moment to challenge a weak resident.

Finally, adult wasps can die while tending their nest before the brood reach maturity, which in essence creates an orphan. Orphaned nests are available for any adult to take over and maintain as their own without the above-mentioned fight for dominance status (Kasuya, 1982). Nest adoption has been also recorded in social wasps besides *Polistes* (e.g. in stenogastrine wasps: Turillazzi, 1985; and vespine wasps: Greene, 1991), but detailed studies of this phenomenon are lacking (Turillazzi, 1991). Paper wasps can receive high pay-offs for alloparenting kin because orphaned young have zero survivorship if not adopted and high survivorship if adopted. Moreover, the pay-off for the alloparent can be substantially greater than simply the survival of kin, because the adopting wasp has an opportunity to become the dominant egg-layer on the nest. Therefore, adoption can have

both indirect fitness benefits (raising kin to become viable reproductive males or new queens) and direct fitness benefits (inheriting a ready-made work-force for rearing newly laid, sexual-destined eggs).

Thus, adoption of orphaned nests by paper wasps may exist as a parental strategy for one or a combination of the following three reasons. First, adoption is a kin-selected strategy in which a hostile environment favors adult wasps taking care of kin other than their own offspring (collateral or non-descendant kin) rather than initiating their own nests. Second, adoption is a fundamentally selfish strategy in which wasps either (1) leave existing colonies in which they are subordinates or (2) simply wait until an appropriate nest becomes orphaned, while avoiding risky care-giving by neither initiating nor helping in other nests. Finally, adoption may represent wasps making the best of a bad situation, such as when predators destroy their original nests and it is too late in the season to start over. In this study, we test these alternatives by examining the fates both of naturally orphaned (abandoned) nests within populations of *Polistes dominulus* and of unoccupied nests artificially transplanted into these populations.

Materials and Methods

Between 1 May and 14 June 1991, all foundress *P. dominulus* queens found on naturally occurring nests at ten distinct rural or suburban sites near Bedford and Carlisle, Massachusetts (USA) were given individually distinctive paint-marks with enamel paint on their thoraces ($n = 294$ queens). Nests of marked queens were censused daily throughout this period, which encompassed the time between nest initiation and the appearance of the first workers. In addition, we periodically recorded the sizes of combs (in total cells) as well as the developmental maturity of their brood (i.e. the stage of the most advanced brood: egg, larva or pupa). Our records enabled us to track both switching of marked foundresses between colonies and joinings of unmarked foundresses with previously established colonies. Throughout the founding period, the combs of some marked foundresses were removed by us or destroyed by birds ($n = 95$ cases overall).

During the founding period, we recorded 34 instances in which original foundresses disappeared from their combs. We denote these nests as 'abandoned nests'. In addition, we transplanted 38 combs removed from one site (as part of the above nest-removal experiment) to nest aggregations of another site 1–10 km away. A 'transplanted nest' was attached to the substrate of its new site by pushing the nest's pedicel into a narrow groove cut into a thin cardboard square, which was then affixed to the substrate with wood glue. Transplanted nests did not significantly differ in cell number from abandoned nests (31.4 cells versus 24.8 cells, respectively; $p > 0.08$, two-tailed t -test) and were made available at approximately the same times that abandoned nests occurred (range of dates = days 7 to 49, mean adoption date = 30.0 days for abandons and range of dates = days 1 to 45, mean adoption date = 30.9 days for transplanted nests). Dates of adoption are given relative to the date of initiation of the study (May 1), so that Day 34 refers to June 3.

We recorded the identities of all marked individuals that adopted either abandoned or transplanted combs. By July 3 1991, we had collected all colonies with original foundresses or adoptive queens and measured, as an estimate of body size, the winglengths (base of tegulum to wing-tip) of all adults (after Noonan, 1981, and Klahn, 1981). Thus, for cases of adoption, we knew the previous nest affiliation of marked queens, the adopting wasps' body size relative to that of other females from the same site, the size and maturity of the

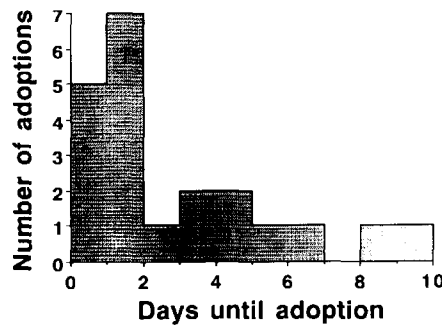


Fig. 1. Frequency distribution of the time (in days) until adoption for the 21 combs that were adopted.

adopted comb, and the date of adoption. We sought to identify: (1) the characteristics of adopting females; and (2) what attributes of unoccupied nests were most attractive to adopters.

Abandoned or transplanted nests were observed at least two weeks after they became available for adoption. As a continuous measure of the 'attractiveness' of unoccupied combs, we calculated, for each such comb, the quantity $1/(\text{days until the comb was adopted})$. If the comb was never adopted, its attractiveness score is zero (i.e. it is assumed that such combs would never have been adopted beyond the censusing period). Thus, attractiveness scores range from zero to one, with higher values indicating greater attractiveness. It should be noted that the 'attractiveness score' is actually directly related to two factors: the intrinsic attractiveness of the comb, and the number of potentially adoptive queens in the population, which may vary over the colony cycle. Unless otherwise noted, all statistical tests are two-tailed.

Results

Of the 72 nests available for adoption, 21 were adopted during the course of the study. Adoptions occurred on average 3.4 days after combs became available (standard deviation = 2.7 days). Fifty-seven percent of adoptions were on the first or second day combs were available (Fig. 1). Since unoccupied nests were censused for two weeks or longer, it thus seems very unlikely that any adoptions would have occurred beyond our censusing period. Orphan nest quality deteriorated with time, in that the brood died or were preyed upon by ants or nearby foundresses.

Characteristics of adoptive queens

We found no evidence that the distance adopting queens dispersed correlated with the date of adoption. Wasps dispersing greater than 10 m (unmarked individuals or marked individuals originating from nests more than 10 m away) adopted at a mean date of 30.0 days, whereas wasps dispersing less than 10 m adopted at a mean date of 28.4 days ($p = 0.78$; two-sample t -test).

Adopting queens did not significantly differ in winglength from other foundresses at the sites of the adopted nests: the mean winglength for adopters (1.25 cm, S.E. = 0.023 cm) was less, but not significantly so, than that of all females at the same site (1.28 ± 0.008 cm;

$p = 0.23$, paired t -test). There was no significant difference in size between adopters of abandoned versus transplanted nests: 1.28 cm for abandoned nests, 1.24 cm for transplanted nests ($p = 0.38$, two-sample t -test). There were also no significant correlations between the sizes of adopters (minus the mean sizes of females at the adoption sites) and size of the comb, date, or comb maturity (Pearson r 's = -0.14 , -0.12 , and $+0.041$, respectively; $p > 0.50$ for all). Thus, there was no tendency for any given size-class of wasps to preferentially become adopters.

Most adopters had earlier lost their nests (7/21 or 33% of adoptions) or switched nests (6/21 or 29% of adoptions) within the same site. However, the remaining 8 adopters (38%) were wasps without any known prior nest affiliation.

Of the six adoptive queens that switched nests, 5 (24% of all adopters) originated from intact nests with multiple foundresses. These adopting queens were smaller, but not significantly so, than the average queen in their site (mean difference = -0.05 cm, $p > 0.28$, one-sample t -test). It is unknown whether the adopters were subordinates on their original nest because we had no behavioral data on their interactions. However, in 3 of the 4 cases where the original wasps were measured (in the remaining case, the original co-foundress disappeared prior to collection), the adopting wasp was smaller than at least one of her initial co-foundresses. Because body size correlates with dominance in *Polistes* in general (Reeve, 1991) and *P. dominulus* in particular (Turillazzi and Pardi, 1977), it seems likely that some, if not all, of these adoptive queens had been subordinates in their original foundress associations.

Characteristics of adopted nests

Abandoned and transplanted nests were available over approximately the same range of dates (7–49 days and 1–45 days, respectively). They did not differ in their attractiveness to adopters: 34% of transplanted nests and 24% of abandoned nests were adopted by queens ($p > 0.40$, χ^2 test). In addition, the dispersal distance for adopters (< 10 m or > 10 m) was not significantly associated with kind of adopted nest (abandoned or transplant; $p > 0.40$; χ^2 test), indicating that transplanted nests were not more likely to be adopted by queens originating from distant sites. For our remaining analyses, we combine the data for abandoned and transplanted combs.

Theoretically, a comb should be selfishly valued according to the product of its probability of surviving and its productivity should it survive. Since nest survivorship per unit time increases dramatically when the first workers emerge (see references in Reeve, 1991), the theoretical value of a comb can be approximated by the product of the colony's (i.e. the adopter's) probability of surviving until the first workers emerge and the nest's size at the time of adoption. The probability of survival until worker emergence is expected to depend on the maturity of the comb, for two reasons. First, when eggs or larvae (as opposed to mostly pupae) are present, an adopter must engage in lengthy and therefore presumably risky foraging trips for pulp and prey to construct the nest and feed the developing larvae (e.g. see Gamboa et al., 1978). Indeed, an analysis of frequencies of single-foundress disappearance for different stages of colony development in undisturbed colonies shows that probabilities of foundress disappearance per day is highest in the egg and larval stages and lowest (by a factor of about 1/3) when there are pupae in the comb (Fig. 2).

Second, the more mature the comb, the closer the time to worker emergence, hence the higher the probability that the adopter and its adopted colony will survive until worker emergence. Thus, theoretically, an adopter should choose (subject to search constraints)

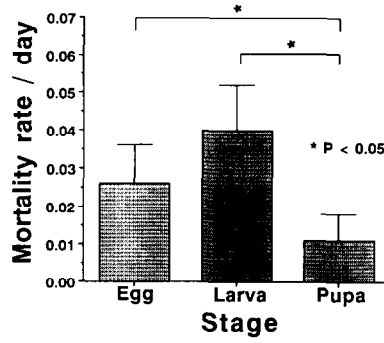


Fig. 2. Probability of foundress disappearance per day as a function of the most mature brood stage present (egg, larvae, or pupae), estimated for 99 naturally-nesting *P. dominulus* single-foundress colonies. For each stage of each nest we calculated the time (in days) to disappearance of the foundress. The reciprocal of this time is an estimate of the probability of disappearance per day (no disappearance = 0). We averaged these probabilities over all nests for each stage to obtain the stage-specific per day disappearance probabilities. Cases where foundresses disappeared the day after their marking were excluded from analyses because of suspicions that the marks injured the foundresses. Per day disappearance probabilities differed among the different stages (Kruskal-Wallis test and multiple comparisons; overall $p = 0.011$).

the nest exhibiting the highest value of sP , where s is the probability of survival until worker emergence and P is the comb size.

We can assign theoretical nest-values to unoccupied *P. dominulus* combs by assuming that the probability of adopter death is approximately constant per unit time for a given stage of development of the adopted comb: that is, $s = (\text{probability of surviving egg stage}) \times (\text{probability of surviving larval stage}) \times (\text{probability of surviving pupal stage}) = (e^{-k_E t_E})(e^{-k_L t_L})(e^{-k_P t_P}) = e^{-k_E t_E - k_L t_L - k_P t_P}$, where k_E, k_L, k_P are the respective per day probabilities of foundress disappearance for the egg, larval, and pupal stages, and t_E, t_L, t_P are the respective remaining durations of these stages. Since the first three developmental stages of *Polistes* brood (egg, larva and pupa) are of approximately equal duration, summing to about forty days (West-Eberhard, 1969; Strassmann and Orgren, 1983), and also since a comb sampled randomly in time will, on average, be halfway through its current stage, t_E, t_L, t_P for an egg stage comb are assumed to be 7, 13, 13, respectively; t_E, t_L, t_P for a larval stage comb are 0, 7, 13, respectively; and t_E, t_L, t_P for a pupal stage comb are 0, 0, 7, respectively. The constants k_E, k_L, k_P are 0.026, 0.040, and 0.011, as empirically estimated for our study population (Fig. 2). Our estimated overall probability that a solitary foundress will survive the entire founding phase in our study population equals $(e^{-0.03 - 0.037 - 0.011 \times 13}) = 0.36$, which is close to the value empirically obtained for three different populations of *P. fuscatus* (Gibo, 1978; Klahn, 1981; Noonan, 1981; Reeve, 1991), a species that is sympatric with *P. dominulus* at our study sites. Thus, a comb's theoretical value to an adoptive queen is equal to:

$$Pe^{-k_E t_E - k_L t_L - k_P t_P} \quad (1)$$

To ascertain how precisely adoption choices match predictions from theoretical nest values, it is useful to ask to what extent use of expression (1) for nest-value improves our ability to

predict adopter choices beyond the use of the comb size P alone or the survival probability s alone. The mean comb size of adopted nests (33.5 cells) was significantly larger than the mean comb size of non-adopted nests (25.6 cells), but only marginally so ($p = 0.04$; two-sample t -test). The mean estimated survivorship potential of adopted nests (0.77) was larger than the survivorship potential of non-adopted nests (0.68), but not significantly so ($p = 0.09$; two-sample t -test). However, the mean theoretical nest-value of adopted nests (28.5) was markedly larger than the mean theoretical nest-value of non-adopted nests (18.2), and the difference is highly significant ($p = 0.009$; two-sample t -test), demonstrating that the theoretical nest-value as a product of comb size and survival probability is the best predictor of adopter choice.

Our model of nest-value predicts a monotonically increasing relationship between the attractiveness of a comb and its theoretical nest-value. However, adopted nests tended to be either low or high in theoretical nest value (Fig. 3), reflected in the fact that a simple linear regression yields a much poorer fit to the scatterplot ($p = 0.023$) than does a third-order polynomial regression ($p = 0.006$), which allows for a concave-up curvature to the regression curve. This U-shaped relationship is also found in the proportions of nests adopted when the 66 nests for which both s and P could be calculated are divided into 6, equal-sized, categories of increasing theoretical value (Fig. 4; simple linear regression: $p = 0.066$; third-order polynomial regression: $p = 0.007$). For the latter regression, the x-coefficient in the regression equation is significantly negative ($p = 0.032$), demonstrating that nests of low theoretical value were more attractive than nests of intermediate theoretical value.

The higher than expected proportion of nests adopted with low theoretical value may represent two (not mutually exclusive) phenomena: (1) the population of orphan-seeking females may be relatively large early in the season when nest-values are low; or (2) early nests may be especially valuable because such nests have more time to attract helpers (joining foundresses) than nests later in the season. The first possibility remains uncertain, because how the pool of potentially adoptive females changes over time due to predation or other mortality factors is unknown. There is, however, some evidence for the second

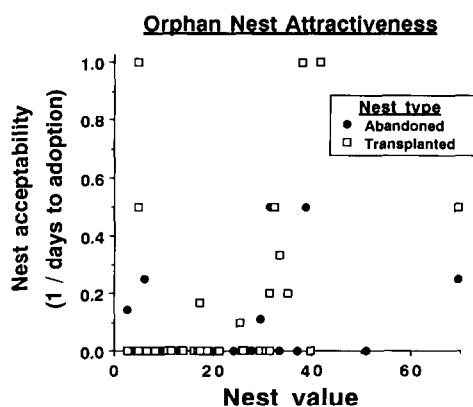


Fig. 3. Unoccupied nest 'acceptability' (see Materials and Methods) as a function of the theoretical value of that nest to adoptive wasps (see Results).

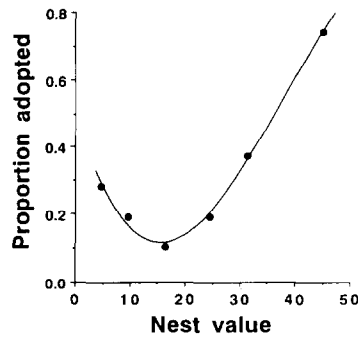


Fig. 4. Proportion of accepted nests as a function of their mean theoretical value. All theoretical nest-values were ordered from lowest to highest. The mean proportion accepted for nests with the lowest eleven theoretical nest-values was plotted against their corresponding mean theoretical nest-value, then the same was repeated for the next lowest eleven nest values, etc., for a total of six nest-value categories ($n = 66$ nests; 11 nests per category). Plotted also is the third-order polynomial regression which closely fits the data.

possibility. In 14% (3/21) of adoptions, the adopter received a joiner. This is probably an underestimate of the true percentage of adopters that acquire joiners since adopters were usually collected on the first or second day after their discovery. Nonacs and Reeve (unpublished data) also found that switching between existing nests in the same *P. dominulus* populations as studied for this experiment tended to occur early in the season. The mean date of switching activity was May 18 and corresponds closely to the first peak of 'attractiveness' for combs, which had a mean date of May 16. Joiners during that time of year were also significantly smaller than the wasps they joined (Nonacs and Reeve, in preparation). Available evidence suggests that smaller joiners tend to be subordinate to resident foundresses (Reeve, 1991). Thus, it seems possible that at least part of the surprisingly high value of early nests results from a greater expectation of acquiring subordinates on such nests.

Both comb size and brood maturity appear to be determinants of the value of the nest. However, an adoptive queen need not assess both variables separately to obtain a reliable estimate of the highest available nest-value, because comb size and maturity are positively correlated (Spearman $\rho = +0.688$; $p < 0.01$). To distinguish which cue is likely to be the more important, we examined partial correlations between nest attractiveness and one nest characteristic when variation in the other characteristic is statistically controlled. Comb size and brood maturity are both also positively correlated with date of season (Spearman ρ for comb size and date = $+0.486$; for comb maturity [1, 2 or 3, corresponding to the stage of the most advanced brood] and date = $+0.746$), so this variable also was statistically controlled. The resulting partial Spearman correlation between nest attractiveness and comb size is $+0.062$ and not significantly different from zero ($p > 0.10$). In contrast, the partial Spearman correlation between nest attractiveness and brood maturity is $+0.254$ and significantly greater than zero ($p < 0.05$). Since date in the season was controlled in the latter correlation, the high attractiveness of mature combs cannot be attributed merely to an increased number of potentially adoptive females relative to the total number of adoptable nests late in the season. Thus, it appears that adoptive queens actively assess the

attractiveness of unoccupied nests primarily by their maturity, perhaps by direct inspection of developmental states of the brood.

Discussion

The results of this study show that adoption of orphaned nests occurs commonly during the colony-founding period of *P. dominulus* and that the wasps are selective in which combs they adopt. Combs that are both large and at an advanced stage of brood development appear to be the most preferred for adoption. The primary proximate cue for adoption seems to be the developmental stage of the nest, with nests of later-instar larvae or pupae on average being significantly preferred over nests with early-instars or eggs. More mature combs tend to be both larger and, perhaps most critically, closer to worker emergence, at which time colony survivorship will dramatically rise (see review in Reeve, 1991). This supports the hypothesis that alloparental care should be preferentially given to offspring requiring the least effort to bring to independence (Nonacs, 1991).

However, the relationship between nest adoption and theoretical nest value (estimated as a function of comb size and survivorship until worker emergence) was best fit by non-linear, U-shaped, regression curves (Figs. 3 and 4). This suggests that small and young orphan nests have a higher than expected chance of being adopted. A possible explanation is that adopted nests early in the year may be more likely to attract a subordinate joiner, which is beneficial to the adoptive queen.

Polistes females tend to nest at their natal site (West-Eberhard, 1969; Klahn, 1979; review in Reeve, 1991) and, in most cases, adopters came from the same site as the abandoned comb. Thus, adopters were likely more related, on average, to the brood of abandoned combs than to the brood of transplanted combs (which were collected from distant sites). However, nests with related brood were not more attractive than nests bearing unrelated or distantly related brood, even though foundresses have the ability to discriminate between related and unrelated brood (Klahn and Gamboa, 1983), suggesting that nest-adoption has not evolved primarily as a strategy to rescue collateral kin. In addition, the 'rescue' hypothesis predicts that queens should not favor any size or developmental class of orphan nests because all brood are in equal need of help and will not survive without an adult presence. Therefore, nest adoption appears to reflect 'selfish' parental interests in that alloparental females significantly favor nests that are close to worker emergence. Such workers will tend the brood of non-maternal, even unrelated, foundresses (Klahn, 1988), probably because they often mistakenly incorporate odor cues of the adopting foundress into their nestmate-recognition template (Gamboa et al., 1986). Any eggs in orphaned combs are likely eaten by the adopting foundress and replaced with her own eggs (Klahn and Gamboa, 1983; Makino, 1985; Klahn, 1988).

Nonacs (1991) predicted that all potential beneficiaries of alloparental care should not be viewed as equal by the alloparent – it should skew effort to those it can identify as providing the most benefit per unit cost. Such costs in wasps may not be primarily in the currency of calories expended, but in terms of the predation risk that the adults must expose themselves to while foraging. This can mean that some parental activities by wasps are 'cheaper' than others. Raising larvae for any length of time may be costly because caterpillar prey must be hunted in vegetation where there are likely to be the most severe mortality risks (i.e. spider webs, mantids, other predators). Indeed, wasp mortality data (Fig. 2) did show that the larval period is the most dangerous time for foundresses.

Conversely, caring for pupae, which require no feeding and only an adult's protective presence on the nest, had a significantly lower mortality rate. An intriguing possibility is that the comb, itself, is not highly valued by wasps. We never observed *P. dominulus* females using previous year's combs although many were structurally intact with no apparent damage or sign of disease. Nor were combs with more cells preferred by adopting wasps after we statistically controlled for the correlated variables of season and brood maturity. In sum, for social wasps it may be that only brood (and particularly older brood) matters in stimulating adoptive behavior: the comb structure itself may only be of ancillary benefit.

The possibility of orphaned nests becoming available to paper wasp females adds to the range of colony-founding options a potential foundress can employ. Adoption is a relatively cheap, if unpredictable, route to becoming a queen on a reasonably well-developed nest. The adult neither pays the cost of foraging for many dependent and voracious young, nor takes the risk of being killed while trying to usurp a dominant from her nest. Adopting a nest clearly is a way in which a foundress who has lost her nest can make the best of a bad situation. Indeed, our data indicate that 33% of the cases of adoption involved foundresses that had lost their nests. However, in the remaining 67% cases, it appears possible that adoption was not a fitness-salvaging, secondary strategy, but instead a primary strategy. Our results suggest two possibilities for what the latter wasps are doing while waiting for their windows of adoptive opportunities to open.

The first may be simply a mortality-risk minimizing strategy of doing nothing but feeding enough to stay alive and healthy. Thirty-eight percent of adoptive females in our study populations had no recorded prior nest affiliation. Although it is possible that some were individuals nesting on nearby combs that our surveys missed, it is unlikely that this can account for all of these apparently 'nest-less' wasps. It seems probable that the majority of such individuals were either local wasps that had no home nest or wasps from a different area migrating in search of opportunities to take over unattended combs (of course, in the latter case we cannot rule out that the immigrating wasps had previously lost nests at their sites of origin).

The second option that a potential adoptive parent may pursue is to start the season as a co-foundress on a nest and work there until she finds an orphaned nest that she can take over. In our data, we have five instances of wasps known to be associated with existing multi-foundress nests moving to adopt another comb. The advantages of this strategy over a purely sit-and-wait strategy are that: (1) if the wasp has to adopt a subordinate role, there is still a possibility that the dominant will die, allowing a co-foundress to 'inherit' the nest; and (2) if no adoptive nest ever becomes available and the dominant survives, the wasp can increase her inclusive fitness by tending kin. The disadvantages of being a subordinate cofoundress versus simply waiting are increased predation risk and less time for looking for orphaned nests because of having to forage for the brood.

In the above discussion we postulate that the adoption-route strategy to gaining a nest is a facultative behavior on the part of fecund *P. dominulus* females. An alternative explanation may be that the reproductive systems of a proportion of females mature only late in the season, such that these females are incapable of producing viable eggs early in the colony cycle. Gadagkar et al. (1990, 1991) have observed that in laboratory-maintained *Ropalidia marginata* wasps, the onset of nest initiation is highly variable across individuals (see also Cibo, 1974, for *Polistes* wasps). Gadagkar (1991a) proposes that late nesters are not physiologically capable of reproducing early in the year and that this delayed reproductive maturity favors cooperatively joining existing nests. Although the proximate effects of Gadagkar's delayed maturity and our opportunistic adoption hypothe-

ses are identical (i.e. a subpopulation of seemingly totipotent wasps not initiating their own nests), the evolutionary explanations are quite different. Gadagkar's model proposes that either through parental manipulation or phenotypic variability, some wasps are extremely predisposed to taking on worker or subordinate roles as the best of a bad situation. The attractiveness of this hypothesis is the mechanism it provides by which a fundamentally solitary-nesting species can evolve into a socially-nesting one. All that is required is enough wasps unable to succeed on their own and that helping an existing nest provides a positive increase in the survivorship of the brood or the nest (Gadagkar, 1990, 1991a).

One problem with Gadagkar's evolutionary scenario is that foundresses that exhibit delayed fecundity will be at a disadvantage in relation to foundresses that exhibit early fecundity while maintaining the helping capacity. This is true because foundresses 'locked' into a delayed maturity will be incapable of seizing immediate personal reproductive opportunities when they arise (e.g. when the dominant foundress dies, or when an orphaned nest is encountered!). Selection thus should strongly act to promote early reproductive competence in foundresses. In fact, there is evidence that helpers are not less fecund than are their dominant nestmates (review in Reeve, 1991). In sum, we believe that our 'sit-and-wait' adoption-strategy hypothesis is currently a better explanation of delayed reproduction in social wasps.

Unlike Gadagkar's (1991a) delayed-maturity mechanism, opportunistic adoption is unlikely to be a major driving force of advanced eusociality, since the latter represents an essentially selfish, minimally-cooperative strategy. More likely is that, to the degree that opportunistic adoption favors the evolution of alloparental care, it is a predisposing factor that allows other advantages of cooperation to begin to operate and to eventually drive social behavior to greater levels of complexity.

The eusocial, multi-generational nature of paper wasps species adds one layer of complexity to parental care that may be absent in non-eusocial species; that is, parents may deliberately use or exploit some offspring as helpers or workers to have greater overall reproductive output. Nevertheless, many of the behaviors exhibited by *P. dominulus* females are at least analogous to behaviors seen elsewhere in nature. Joining an established, breeding female to help raise kin is a widespread phenomenon (Wilson, 1975). Cooperative breeding occurs in scrub jays (Woolfenden and Fitzpatrick, 1984), acorn woodpeckers (Koenig and Mumme, 1987) and many mammalian carnivores, to give just a few examples. Cooperation changing to attempted displacement or usurpation of the dominant within social groups occurs with equal ubiquity. In a striking example of adaptive convergence of alloparental strategies between cooperatively breeding birds and adoptive *P. dominulus* females, Ligon (1981) found that subordinate green woodhoopoes help rear offspring (sometimes unrelated) that will later help the original helper rear its young!

The ecology of adopting orphaned young has not received the rigorous scrutiny of cooperative social and reproductive behavior. However, it is clear that adoptive behavior occurs in a wide variety of species, although it appears to vary across species in whether offspring, the alloparents, or both parties gain the greatest benefit (Riedman, 1982; Nonacs, 1991; Pierotti, 1991; this study). In *P. dominulus* the adopting parent appears to stand to gain the greatest benefit in that she may become queen to a pliant workforce that will raise her eggs. However, as our study terminated prior to the end of the season, we cannot be definitive about the adopting parent's eventual success. Previous work on polistines has shown that nest usurpers are often eventually displaced from the nest by the resident female's adult offspring and therefore have somewhat diminished reproductive success (Klahn, 1988). However, the consequences of any given parental decision are not

impenetrable to experimental scrutiny. The ease with which substantial field populations can be located, marked, followed and manipulated makes paper wasps an almost ideal group for tests of parental investment theory. It may be that wasps sitting on their nests will provide us with the tool to solve some of the most nettlesome problems in the evolution of parental care.

Acknowledgements

We thank E.O. Wilson for his gracious support and encouragement throughout the project and all the people at the Concord Field Station whose offices we used and who refrained from killing any and all wasps during our study! H.K.R. was also supported by a Junior Fellowship from the Harvard University Society of Fellows.

References

- Evans, H.E., 1958. The evolution of social life in wasps. *Proc. 10th Int. Congr. Entomol.*, 2: 449–457.
- Gadagkar, R., 1990. Evolution of eusociality: the advantages of assured fitness returns. *Phil. Trans. R. Soc. Lond. B*, 329: 17–25.
- Gadagkar, R., 1991a. Demographic predisposition to the evolution of eusociality: a hierarchy of models. *Proc. Natl. Acad. Sci. USA* 88: 10993–10997.
- Gadagkar, R., 1991b. *Belonogaster*, *Miscocyttarus*, *Parapolybia*, and independent-founding *Ropalidia*. In: K.G. Ross and R.W. Matthews (Editors), *The Social Biology of Wasps*, Cornell University Press, Ithaca, pp. 149–190.
- Gadagkar, R., Bhagavan, S., Malpe, R. and Vinutha, C., 1990. On reconfirming the evidence for pre-imaginal caste bias in a primitively eusocial wasp. *Proc. Indian Acad. Sci.* 99: 141–150.
- Gadagkar, R., Bhagavan, S., Chandrashekara, K. and Vinutha, C., 1991. The role of larval nutrition in pre-imaginal biasing of caste in the primitively eusocial wasp *Ropalidia marginata* (Hymenoptera: Vespidae). *Ecol. Entomol.* 16: 435–440.
- Gamboa, G.J., 1978. Intraspecific defense: Advantage of social cooperation among paper wasp foundresses. *Science* 199: 1463–1465.
- Gamboa, G.J., Heacock, B.D. and Wiltjer, S.L., 1978. Division of labor and subordinate longevity in foundress associations of the paper wasp, *Polistes metricus* (Hymenoptera: Vespidae). *J. Kans. Entomol. Soc.* 51: 343–352.
- Gamboa, G.J., Reeve, H.K. and Pfennig, D.W., 1986. The evolution and ontogeny of nestmate recognition in social wasps. *Ann. Rev. Entomol.* 31: 431–455.
- Gibo, D.L., 1974. A laboratory study on the selective advantage of foundress associations in *Polistes fuscatus*. *Can. Entomol.* 106: 101–106.
- Gibo, D.L., 1978. The selective advantage of foundress associations in *Polistes fuscatus* (Hymenoptera: Vespidae): A field study of the effects of predation on productivity. *Can. Entomol.* 110: 519–540.
- Greene, A., 1991. *Dolichovespula* and *Vespula*. In: K.G. Ross and R.W. Matthews (Editors), *The Social Biology of Wasps*, Cornell University Press, Ithaca, pp. 263–305.
- Kasuya, E., 1982. Take-over of nests in a Japanese paper wasp, *Polistes chinensis antennalis* (Vespidae: Hymenoptera). *Appl. Entomol. Zool.* 17: 427–431.
- Klahn, J.E., 1979. Philopatric and nonphilopatric foundress associations in the social wasp *Polistes fuscatus*. *Behav. Ecol. Sociobiol.* 5: 417–424.

- Klahn, J.E., 1981. Alternate reproductive tactics of single foundresses of a social wasp, *Polistes fuscatus*. Ph.D. thesis, Univ. Iowa, Iowa City. 156pp.
- Klahn, J.E., 1988. Intraspecific comb usurpation in the social wasp *Polistes fuscatus*. Behav. Ecol. Sociobiol. 23: 1–8.
- Klahn, J.E. and Gamboa, G.J., 1983. Social wasps: discrimination between kin and non-kin brood. Science 221: 482–484.
- Koenig, W.D. and Mumme, R.L., 1987. Population Ecology of the Cooperatively Breeding Acorn Woodpecker. Princeton University Press, Princeton, NJ.
- Ligon, J.D., 1981. Demographic patterns and communal breeding in the Green Woodhoopoe, *Phoeniculus purpureus*. In: R.D. Alexander and D.W. Tinkle (Editors), Natural Selection and Social Behavior, Chiron Press, New York, pp. 231–243.
- Makino S., 1985. Foundress-replacement on nests of the monogynic paper wasp *Polistes biglumis* in Japan (Hymenoptera: Vespidae). Kontyu. 53: 143–149.
- Noonan, K.M., 1981. Individual strategies of inclusive-fitness-maximizing in *Polistes fuscatus* foundresses. In R.D. Alexander and D.W. Tinkle (Editors), Natural Selection and Social Behavior, Chiron Press, New York, pp. 18–44.
- Nonacs, P., 1991. Alloparental care and eusocial evolution: the limits of Queller's head-start advantage. Oikos 61: 122–125.
- Pierotti, R., 1991. Infanticide versus adoption: an intergenerational conflict. Am. Nat. 138: 1140–1158.
- Queller, D.C., 1989. The evolution of eusociality: reproductive head starts of workers. Proc. Natl. Acad. Sci. USA 86: 3224–3226.
- Reeve, H.K., 1991. *Polistes*. In: K.G. Ross and R.W. Matthews (Editors), The Social Biology of Wasps, Cornell University Press, Ithaca, pp. 99–148.
- Riedman, M.L., 1982. The evolution of alloparental care and adoption in mammals and birds. Quart. Rev. Biol. 57: 405–435.
- Strassmann, J.E. and Orgren, C.F., 1983. Nest architecture and brood development times in the paper wasp *Polistes exclamans* (Hymenoptera: Vespidae). Psyche. 90: 237–248.
- Turillazzi, S., 1985. Colonial cycle of *Parischnogaster nigricans serrei* (Du Buysson) in West Java (Hymenoptera, Stenogastrinae). Ins. Soc. 32: 43–62.
- Turillazzi, S., 1991. The Stenogastrinae. In: K.G. Ross and R.W. Matthews (Editors), The Social Biology of Wasps, Cornell University Press, Ithaca, pp. 74–98.
- Turillazzi, S. and Pardi, L., 1977. Body size and heirarchy in polygynic nests of *Polistes gallicus* (L.) (Hymenoptera: Vespidae). Monit. Zool. Ital. 11: 101–112.
- West Eberhard, M.J., 1969. The social biology of polistine wasps. Univ. Mich. Mus. Zool. Misc. Publ. 140: 1–101.
- Wilson, E.O., 1971. The Insect Societies. Belknap Press of Harvard Univ. Press, Cambridge, Mass., 548 pp.
- Wilson, E.O., 1975. Sociobiology. Belknap Press of Harvard Univ. Press, Cambridge, Mass.
- Woolfenden, G.E. and Fitzpatrick, J.W., 1984. The Florida Scrub Jay: Demography of a Cooperative Breeding Bird. Princeton University Press, Princeton, NJ.