Benefits of foundress associations in the paper wasp *Polistes dominulus*: increased productivity and survival, but no assurance of fitness returns

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Successful *Polistes dominulus* nests can be started by one or more nest founding queens (foundresses). Consequently, there is much interest in the specific benefits that induce cooperation among foundresses. Here, we experimentally demonstrate one major benefit of cooperation, namely that multiple foundresses increase colony productivity. This increase is close to the value predicted by subtracting the productivity of undisturbed single-foundress colonies from the productivity of undisturbed multiple-foundress colonies. However, we found no evidence that an associating foundress' contribution to colony growth is preserved if she disappears (assured fitness returns). Our correlational data suggest that cooperation provides survival benefits, multiple-foundress colonies are more likely to survive to produce offspring than are single-foundress colonies, and individual foundresses in multiple-foundress groups are less likely to disappear before worker emergence than foundresses nesting alone. Therefore, association provides substantial productivity and survival benefits for cooperating foundresses. *Key words:* eusociality, inclusive fitness, kin selection, reproductive skew. *[Behav Ecol 14:510–514 (2003)]*

O ne of the central questions of research on social behavior is why do individuals rear offspring cooperatively? This question is particularly pertinent when every individual appears capable of independent reproduction, as in associations of *Polistes* paper wasp queens. Numerous models have been developed to predict the circumstances that favor association (Reeve, 1991; Reeve and Emlen, 2000; Reeve and Ratnieks, 1993). The most recent and general of these models derived from transactional skew theory predict that group formation will be favored if the number of offspring reared by a dominant nesting alone plus the number of offspring reared by a subordinate nesting alone is less than the number of offspring they would rear while associating. More generally, groups of size N will be stable if the number of offspring reared by a group of $N - 1$ individuals plus the number of offspring reared by a subordinate nesting alone is less than the number of offspring reared by a group of N individuals (Reeve and Emlen, 2000). Surprisingly, the relatedness of associating individuals does not influence this inequality. As long as there is a net benefit of association, group members are predicted to divide reproduction so every individual also benefits. Therefore, all group members have the same interests regarding whether or not they should associate.

Many studies have used correlational data to show that multiple-foundress *Polistes* colonies are more successful than are single-foundress colonies. They are usurped less often (Gamboa, 1978; Klahn, 1988), survive better (Gibo, 1978; Metcalf and Whitt, 1977), and are more productive than are single-foundress colonies (Gamboa, 1980; West-Eberhard, 1969). However, without experimental studies, it remains unclear whether the presence of additional foundresses increases survivorship and productivity, while decreasing usurpation, or whether many foundresses simply join nests with superior characteristics. Further, increased survival of multiple-foundress colonies relative to single-foundress colonies is not necessarily a benefit of cooperation. Increased colony survival is an inevitable consequence of association if each cooperating individual has an equal survival probability as do solitarily nesting individuals. Of course, it is more likely that at least one foundress from a two-foundress colony will survive than at least one foundress from a single-foundress colony. However, this increased survival will only produce a net fitness benefit if there are synergistic effects of association: (1) if individual foundresses on multiple-foundress nests are more likely to survive than foundresses who nest alone (the survival insurance hypothesis: Nonacs and Reeve, 1995; Reeve, 1991; proof in Appendix), or (2) if some of the foundress' contribution to the colony is preserved should she disappear (assured fitness returns hypothesis: Queller, 1989; Gadagkar, 1990).

Under the survival insurance hypothesis, group formation is favored by kin selection because a provisioning subordinate reduces the workload of a dominant, increasing the probability that at least one foundress survives until worker emergence and ensuring that some larvae will survive to maturity. Under the assured fitness returns hypothesis, even short periods of work by a subordinate increases the number of surviving larvae. These surviving larvae will be related to the subordinate either because they are her own or are offspring of a genetically related cofoundress. Both hypotheses apply only to colonies in which all foundresses reproduce and/or foundresses are related. Therefore, they potentially apply to most species of cofounding insects, including *Polistes* wasps (Ross and Carpenter, 1991).

In this article, we use an experimental approach to determine the effects of multiple foundresses on colony productivity, by comparing the productivity of multiple-foundress colonies in which all foundresses were removed early in the founding period (removal colonies) to the productivity of single and multiple-foundress colonies. If the
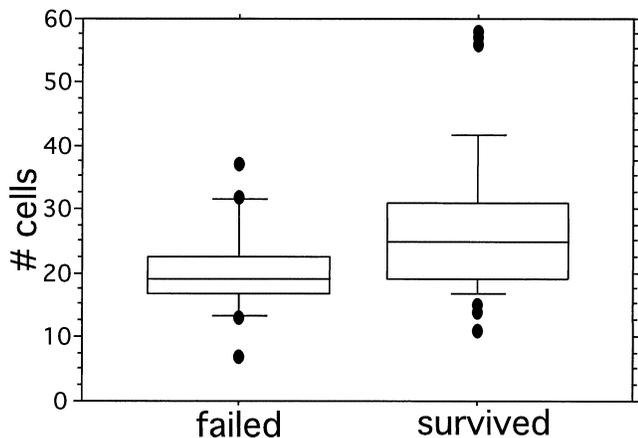
Figure 1
Colony size was measured in 1 June. All foundresses disappeared from "failed" colonies between 1 June and 1 July. At least one foundress remained on "survived" colonies until 1 July.

presence of multiple foundresses causes the increase in colony productivity, removal and single-foundress colonies should have similar productivity. If the presence of multiple foundresses is merely correlated to increased productivity, removal and multiple-foundress colonies should have similar productivity. An intermediate result would indicate that both effects contribute.

We also investigate whether increased survival of multiple-foundress nests translates into inclusive fitness benefits for all individuals in an association by examining the assured fitness returns and survival insurance hypotheses. Wasps often die before their offspring eclose and, on a single wasp nest, all these larvae would be lost. On a multiple wasp nest, other wasps could raise these offspring to maturity, preserving the dead wasp's prior investment. Such assured fitness returns for short periods of work could provide a significant benefit to association. Here, we examine whether fitness returns are assured by testing whether a subordinate's contribution to colony growth is maintained after she is removed. We also examine whether cooperating individuals have a higher probability of survival than individuals who nest alone.

METHODS

We studied *P. dominulus* populations in Ithaca, New York, in 2000 and Boston, Massachusetts, in 1993. In early spring, *P. dominulus* nests are founded by one to six foundresses who cooperate in nest building and brood care. When multiple foundresses cooperate in nest foundation, they form a linear dominance hierarchy. The most dominant foundress physically dominates subordinates and lays the largest fraction of eggs (Reeve, 1991).

We studied naturally nesting colonies of *P. dominulus* very soon after the nests were founded. First, we marked all foundresses on the thorax with enamel paint for easy identification. After marking, we used stereotyped interactions such as mounting to identify foundress dominance rank (see Tibbetts and Reeve, 2000). We removed all subordinate foundresses from half the multiple-foundress nests, creating three classes of colonies: single-foundress, multiple-foundress, and removal (multiple-foundress colonies from which all subordinates were removed).

To prevent other wasps from joining the colonies and altering the manipulations, we removed all unmarked wasps who joined the colonies between subordinate removal and the

day of first worker emergence. Productivity was estimated by cell number. In Ithaca, we counted the total number of cells in each comb that had contained pupae (over the entire season). In Boston, we counted the number of cells in each nest on 23 June (end of the founding period). For statistical analysis, cell counts were transformed by log 10 for normality, but SDs and means are reported by using untransformed cell counts. Reported productivities are only for colonies that survived until worker emergence. Colonies were scored as "failed" if all foundresses disappeared before worker emergence. Whole-nest predation is not included in this category, because many studies have shown that rates of whole-nest predation do not systematically differ between single- and multiple-foundress nests (review in Reeve, 1991; this study $\chi^2 = 0.52$, $p = .77$, df = 2). Factorial ANOVA was used, and all post hoc ANOVA analyses used Bonferroni correction. Two-tailed parametric statistical tests were used in all analyses unless otherwise noted.

Ithaca

We followed 50 single-foundress and 48 multiple-foundress colonies from nest foundation. On 1 June 2000, we removed all subordinate foundresses from 24 multiple-foundress colonies (mean number of subordinates removed, 2.62; range, 1–5) to create removal colonies.

Every colony was censused weekly throughout the study. Censuses were performed early in the morning when all colony members were present. Every week, the nest size and numbers and identities of all wasps were recorded. Weekly censuses continued until 10 September 2000, when new wasps were no longer eclosing and gynes (future foundresses) were cannibalizing larvae.

Boston

On 3–5 June 1993 all subordinate foundresses were removed from 10 of the multiple-foundress nests (mean number of subordinates removed, 1.7; range, 1–3). On 5 June, there were 16 single-foundress, 10 multiple-foundress, and 15 removal colonies. On 3 June, the number of cells in each colony was measured. One 23 June, colonies were censused and the number of cells in each colony was measured again. Workers emerged on all colonies by 10 July.

RESULTS

Colony failure

Colony failure was higher in single than in multiple-foundress colonies at both study sites. In Ithaca, from 1 May until 1 June, all foundresses disappeared from 14 of 50 single-foundress nests, but only one of 48 multiple-foundress nests ($\chi^2 = 12.43$, $p = .0004$). Nests that failed after 1 June tended to be smaller on 1 June than did nests that did not fail after 1 June (df = 66, $t = -3.05$, $p = .003$). Therefore, smaller nests were more likely to fail. This result is somewhat misleading because multiple-foundress colonies were larger on 1 June and also failed less often. However, within single-foundress colonies, smaller nests were more likely to fail than were larger nests (df = 49, $t = -2.34$, $p = .03$) (Figure 1). There were two multiple-foundress colonies that failed during this period, and they also tended to be smaller than colonies that succeeded, although the difference was not significant (df = 14, $t = -1.41$, $p = .18$).

Individual foundresses on single-foundress nests were more likely to disappear before 1 June than were individual foundresses on multiple-foundress nests (single, 14 of 49 [28% disappearance]; multiple, 16 of 111 [15% disappear-

ance]). To control for differences in failure rate and frequency of multiple-foundress colonies across locations, we compared the mean disappearance rate of individual foundresses from multiple-foundress versus single-foundress colonies in each of the 10 locations. These results further indicated that there was a higher foundress disappearance rate on single-foundress nests than on multiple-foundress nests (Wilcoxon signed-rank test: $Z = -2.13$, $p = .03$). Dominant and subordinate foundresses were pooled in this analysis.

Effect of number of foundresses on colony productivity

Ithaca
There were significant differences in colony size at removal across the three classes of colonies ($F_{2,41} = 9.87$, $p = .0003$; single, SD = 5.5, $n = 16$; multiple, SD = 10.8, $n = 12$; removal, SD = 12.4, $n = 16$) (Figure 2a, Table 1). Bonferroni post hoc analysis shows that multiple-foundress and removal colonies were similarly sized ($p = .68$). However, single-foundress colonies were smaller than both removal ($p = .0002$) and multiple-foundress colonies ($p = .0015$).

At the end of the season, the three classes of colonies had significantly different sizes ($F_{2,41} = 10.4$, $p = .0002$; single, SD = 63, $n = 16$; multiple, SD = 111, $n = 12$; removal, SD = 45, $n = 16$) (Figure 2a), but the Bonferroni post hoc analysis shows that single-foundress and removal colonies were similarly sized ($p = .16$), whereas multiple-foundress colonies were larger than both single-foundress ($p = .003$) and removal ($p < .0001$) colonies.

In the 2 weeks after subordinate removal, these three classes of colonies grew at different rates ($F_{2,43} = 9.8$, $p = .0002$; single, SD = 11, $n = 18$; multiple, SD = 32, $n = 11$; removal, SD = 4, $n = 17$). Removal colonies grew much more slowly than multiple-foundress colonies ($p = 0.0007$) and single-foundress colonies ($p = .0004$), whereas single and multiple-foundress colonies grew at a similar rate ($p = .77$).

The change in colony size from the day of subordinate removal until the end of the season showed a similar pattern ($F_{2,41} = 11.9$, $p < .0001$; single, SD = 61, $n = 16$; multiple, SD = 106, n = 12; removal, SD = 9.5, $n = 16$). Removal nests grew less than single-foundress ($p = .004$) and multiple-foundress ($p < .0001$) colonies, whereas single and multiple-foundress colonies grew similarly ($p = .05$).

Boston
Analogous trends were found in the Boston site. The initial sizes of the three classes of colonies were different ($F_{2,26} = 11.5$, $p = .0003$; single, SD = 9.7, $n = 9$; multiple, SD = 20, $n = 9$; removal, SD = 13, $n = 12$) (Figure 2b, Table 2). Bonferroni post hoc analysis shows this difference occurs because single-foundress colonies were smaller than multiple-foundress ($p = .0004$) and removal ($p = .0002$) colonies, whereas removal and multiple-foundress colonies were similarly sized ($p = .93$). After subordinate removal, these three classes of colonies grew at different rates ($F_{2,27} = 15.9$, $p < .0001$; single, SD = 10, $n = 9$; multiple, SD = 8, $n = 9$; removal, SD = 6, $n = 12$). Removal colonies grew much more slowly than did single-foundress ($p = .0002$) and multiple-foundress ($p < .0001$) colonies, whereas single- and multiple-foundress colonies grew at similar rates ($p = .44$). By 23 June, the three classes of colonies were different sizes ($F_{2,27} = 4.1$, $p < .03$; single, SD = 15, $n = 9$; multiple, SD = 20, $n = 9$; removal, SD = 12, $n = 12$) (Figure 2b). The post hoc analysis shows similar trends to the Ithaca data, although the results are not as strongly significant, likely owing to the smaller sample size and shorter experimental period. Multiple-foundress colonies were larger than single-foundress
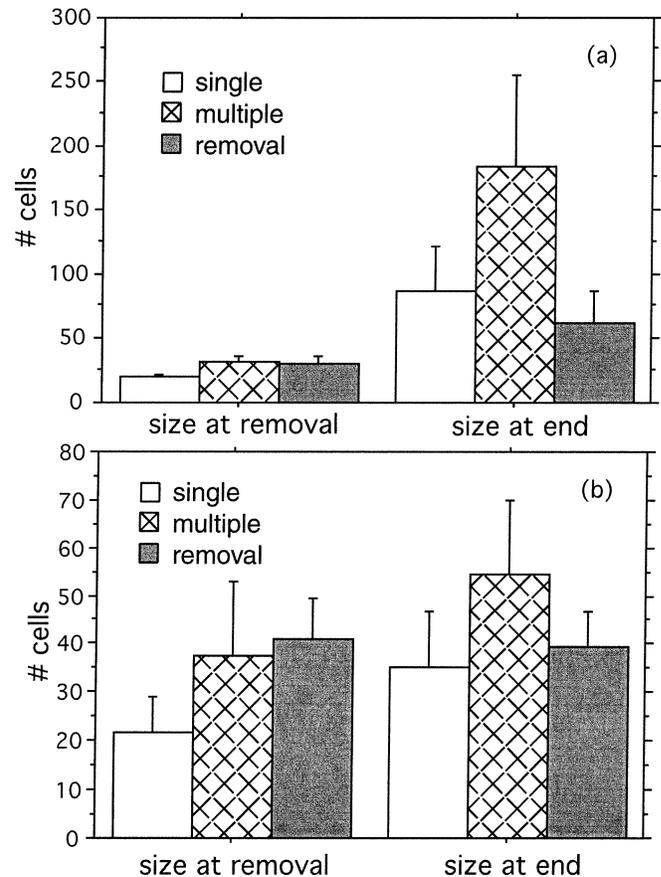
Figure 2
(a) Ithaca. The sizes of single, multiple-foundress, and removal colonies on the day of subordinate removal versus the size of colonies at the end of the colony cycle (+ 95% CI). (b) Boston. The sizes of single, multiple-foundress, and removal colonies on the day of subordinate removal versus the size of these colonies 18 days after removal (+ 95% CI).

($p = .009$) and removal ($p = .05$) colonies, whereas single-foundress and removal colonies were similarly sized ($p = .33$).

In the Boston removal colonies, six nests actually had fewer cells on the last census than on the first census. Interestingly, nests that were larger than the median size at the first census exhibited larger reductions in nest size (mean change, −6.6 cells) than did nests that were smaller than the median nest size at the first census (mean change, 1.5 cells; Mann Whitney test: $z = -2.0$, $p = .04$, $n = 11$). These reductions in nest size were most likely on nests that originally had three or more foundresses: The mean change in cell number was 0.13 cells for colonies that originally contained two foundresses ($n = 8$) and −8.3 cells for colonies with more than two foundresses ($n = 3$; Mann Whitney test: $z = -2.04$, $p = .040$). These data indicate that on a large nest, especially one that had been co-constructed by at least two other foundresses, the lone alpha foundress was especially likely to use excess cells and perhaps even cannibalize excess larvae to care for a smaller number of larvae.

DISCUSSION

Productivity

The presence of subordinates through the entire founding phase significantly increased colony productivity. There was no evidence that subordinates were attracted to nests destined

Table 1
Summary of survival and productivity data: Ithaca 2000

Treatment	N	No. of colonies failed (1 May−1 June)	No. of foundresses disappeared (1 May−1 June)	No. of colonies failed after 1 June	No. of colonies predated	No. of cells at removal (1 June)	Growth (1−15 June)	Final no. of cells	Growth (1 June−end of season)
Single	50	14	14/50	14	6	20	11	88	68
Multiple	24	1	16/111	2	9	32	20	185	155
Removal	24	—	—	4	4	33	3	63	32

to have higher productivity. This result is important because it implies that the increase in group output owing to the efforts of subordinate foundresses can be accurately computed by subtracting the productivity of undisturbed single-foundress colonies from that of undisturbed multiple-foundress colonies (e.g., using the mean Ithaca colony sizes from Table 1: 184 cells − 88 cells = 96 cells). Therefore, multiple-foundress colonies had approximately 2.62 subordinates who contributed an average of 96 cells to their colonies.

Survivorship

Early in the founding phase, multiple-foundress colonies survived much better than did single-foundress colonies. The survival advantage of multiple-foundress colonies in this *P. dominulus* population matches numerous other studies that have demonstrated that colonies with more foundresses are less likely to fail (Gibo, 1978; Metcalf and Whitt, 1977; Queller and Strassmann, 1988; review in Reeve, 1991).

However, as described earlier, cooperation provides a survivorship benefit only if (1) individual foundresses on multiple queen nests (e.g., the dominant foundresses) have a higher probability of survival than foundresses who nest alone (survival insurance hypothesis, see Appendix), or (2) some of the foundress' contribution to the colony is preserved after she disappears (assured fitness returns hypothesis).

We found that foundresses on multiple-foundress nests were more likely to remain on their nest all season than were foundresses on single-foundress nests. This difference probably occurs because subordinate foundresses perform more dangerous and energetically costly tasks, (Pratte, 1989; West-Eberhard, 1969), so dominant foundresses survive better than both subordinate and solitary foundresses (Pfennig and Klahn, 1985).

A potential problem with the foundress disappearance data is that we do not know what happens to foundresses that disappear. Foraging-related mortality is thought to be the primary cause of foundress disappearance (Nonacs and Reeve, 1995; Strassmann, 1981). However, we found that smaller singly founded nests failed more than larger singly founded nests, indicating that the cause of foundress disappearance may be more complicated than foundress

Table 2
Summary of survival and productivity data: Boston 1993

Treatment	N	No. of colonies failed (3−23 June)	No. of cells at removal (3 June)	No. of cells at removal (23 June)	Growth (3−23 June)
Single	16	7	22	35	13
Multiple	10	1	37	54	17
Removal	15	3	41	39	−2

death. Perhaps foundresses on small less-successful nests abandon these nests to pursue other reproductive strategies. We observed a marked single-foundress abandon her small shaded colony to join a larger removal colony 100 m away. Further, Nonacs and Reeve (1995) found that solitary foundresses readily pursue alternative strategies such as usurping, adopting, or joining other nests. More studies are necessary to clarify the reproductive strategies of *Polistes* wasps, but these results indicate that these strategies may be more varied than previously thought.

Assured fitness returns

We found no significant evidence of assured fitness returns. When subordinates were removed before worker emergence, their contribution to colony productivity was not preserved at either Boston or Ithaca. Although multiple-foundress and removal colonies were larger than were single-foundress colonies at subordinate removal, growth of removal colonies stagnated. In fact, larger removal colonies often decreased in size. By the end of the season, removal colonies were similar in size to single-foundress colonies. Therefore, a month of work by subordinates had no lasting impact on nest size.

One month is about half the founding period in *P. dominulus*, so colonies contained eggs and small- and medium-sized larvae at subordinate removal. The first half of the founding phase probably requires less time and energy than does the last half, as provisioning large larvae with caterpillar prey is thought to be more costly than nest building and egg laying. Colony size during the early founding stage may be limited by a foundress' prediction of how many wasps the colony can rear to maturity rather than by early labor and fertility constraints (Wenzel, 1993). Therefore, it is not surprising that early subordinate contributions are not preserved by a lone dominant foundress.

If a subordinate works for a larger fraction of the founding stage, it is more likely that her contribution will be preserved after she disappears. For example, if she helps rear enough large larvae, the remaining foundresses may be able to rear more total offspring by using some partially reared larvae as food stores. Feeding the larvae to other offspring may allow the remaining foundresses to rear more total offspring and effectively preserve some of the subordinate's investment (Field et al., 2000). Indeed, this may account for some of the nest-size reduction of removal colonies in our Boston experiments. Interestingly, foundresses on removal nests at both sites had higher survivorship (although not significantly) than did single foundresses over the same time period, raising the possibility that brood cannibalism reduced their exposure to foraging risks; this would represent a conversion of assured fitness returns from increased productivity to increased foundress survival. The preservation of a subordinate's investment may also depend on specific environmental conditions and food availability. In an exceptionally good year, foundresses may be able to care for more larvae and preserve

some of a departed foundress' investment. Investment preservation may also increase with the number of foundresses remaining on a colony, because of the increased likelihood that a foundress will be present to preserve past investments.

Therefore, associating foundresses receive benefits through increased foundress and colony survival, as well as increased colony productivity. However, we found no evidence that a foundress' productivity contributions were preserved after her disappearance. Some additional questions regarding the benefits of association remain, particularly in the area of assured fitness returns. Are fitness returns assured after foundress disappearance in other contexts (e.g., when foundresses disappear later in the season, or when there are more foundresses)? Are fitness returns in the form of increased survival of remaining foundresses or increased productivity of the remaining colony? Despite these questions that remain, it is clear that association provides substantial benefits for cofoundresses.

APPENDIX

Foundress survival and joining benefits

Reeve (1991) showed that enhanced renesting success of foundress associations relative to single foundresses after whole-nest predation does not necessarily provide an inclusive fitness benefit for joining a foundress association. Here, we show that a lowered probability of colony failure owing to chance loss of all foundresses before worker emergence does not provide an inclusive fitness benefit unless individual foundress survival is increased by the association. Assume that a solitary foundress has a probability, s, of surviving until worker emergence. If she survives to worker emergence, the colony survives into the future with probability 1.0 and has a total productivity, K. However, if the foundress dies before worker emergence, the entire colony dies. Also assume that if a potential subordinate foundress joins a dominant foundress that is related by r, both foundresses have independent probabilities, s, of surviving to worker emergence. The colony fails only if both die before worker emergence. If both foundresses survive (probability $= s^2$), the subordinate gets a fraction, p, of the total output, $2K$ (thus, output is linearly related to the number of surviving foundresses). If one foundress dies, the other obtains all of the reproduction, but the nest is assumed no more productive than is a solitary foundress colony (i.e., there are no assured fitness returns).

By Hamilton's rule, joining by the potential subordinate is favored when

$$s^2p2K + s(1-s)K - sK + r[s^2(1-p)2K + (1-s)sK - sK] > 0$$

which reduces to

$$ks^2[2p(1-r) - 1 + r] > 0.$$

The latter can be true only if $p > .5$, which can never occur. If $p > .5$, the dominant foundress would be favored to leave the association. Thus, the association could not be stable.

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