Insurance-based advantages for subordinate co-foundresses in a temperate paper wasp

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Recent explanations for the evolution of eusociality, focusing more on costs and benefits than relatedness, are largely untested. We validate one such model by showing that helpers in foundress groups of the paper wasp *Polistes dominulus* benefit from an insurance-based mechanism known as Assured Fitness Returns (AFRs). Experimental helper removals left remaining group members with more offspring than they would normally rear. Reduced groups succeeded in preserving the dead helpers' investment by rearing these extra offspring, even when helper removals occurred long before worker emergence. While helpers clearly gained from AFRs, offspring of lone foundresses failed after foundress death, so that AFRs represent a true advantage for helpers. Smaller, less valuable offspring were probably sacrificed to feed larger offspring, but reduced groups did not preferentially attract joiners or increase their foraging effort to compensate for their smaller workforce. We failed to detect a second insurance-based advantage, Survivorship Insurance, in which larger groups are less likely to fail than smaller groups. We suggest that through their use of small offspring as a food store to cope with temporary shortages, wasps may be less susceptible than vertebrates to offspring failure following the death of group members.

Keywords: assured fitness returns; wasps; eusociality; cooperative breeding; *Polistes*

1. INTRODUCTION

The evolution of eusociality is a central problem in evolutionary biology. The celebrated haplodiploidy hypothesis of Hamilton (1964), that the decisive factor is the 3/4-relatedness between female hymenopterans, has been largely superseded by models focusing on ecological costs and benefits, but these require empirical validation. Here, we test one such model that is based on insurance, using *Polistes* paper wasps, a model system for social evolution research.

An obligate period of parental care poses a problem when adult lifespan is short compared with the time needed for offspring to become independent (Queller 1989, 1994, 1996; Gadagkar 1990; Strassmann & Queller 1989). A lone parent then has only a small chance of successful reproduction. For example, among 19 species of polistine wasps, 38–100% of nests with lone foundresses fail before producing adult offspring (Queller 1996). This demographic constraint can provide helpers with insurance-based advantages over lone foundresses, even when relatedness between group members is low and direct reproduction is monopolized by a single, dominant group member (Reeve 1991; Queller 1994). Insurance-based advantages are likely to have been significant in both the origin and maintenance of eusociality and other forms of social behaviour (Queller 1994, 1996; Kukuk *et al.* 1998; Field *et al.* 2000). Since they do not assume haplodiploidy, they are potentially relevant to both vertebrates and invertebrates.

One such advantage, known as Assured Fitness Returns (AFRs; Gadagkar 1990), occurs when offspring that a helper has only part-reared can be brought to adulthood by surviving group members after the helper dies. Models suggest that this mechanism can favour helping even when helper-offspring relatedness is very low (Gadagkar 1990). We have previously shown that AFRs give helpers a significant fitness advantage over lone foundresses in the facultatively eusocial hover wasp *Liostenogaster flavolineata* (Field *et al.* 2000).

For AFRs to occur, the smaller group remaining after a helper's death must finish rearing the extra offspring that she contributed, in addition to the number of offspring that a smaller group would normally be able to rear. We suggested that reduced groups of *L. flavolineata* were able to preserve the investment of experimentally removed nest-mates through a combination of increased short-term helper recruitment and the sacrifice of smaller, less valuable offspring to feed larger ones (Field *et al.* 2000). Remaining group members did not appear to increase their foraging effort in order to maintain extra offspring, a response that would probably have increased helper mortality rates (e.g. Cant & Field 2001).

A second potential insurance-based advantage of helping, which can operate at the same time as AFRs, is known as 'survivorship insurance' (SI). SI operates if the chance of total reproductive failure due to the deaths of all carers is reduced in larger groups (Nonacs 1991; Reeve 1991; Queller 1994; Reeve & Nonacs 1997). In this paper, we test experimentally whether subordinate helpers have insurance-based advantages in foundress groups of the polistine wasp *Polistes dominulus* prior to worker emergence. By removing one to two helpers experimentally, we are able to assess the extent to which remaining group members can preserve the investments of their dead nest-mates via AFRs, and whether experimentally reduced groups suffer increased nest failure rates, as expected if SI operates.

The biology of the temperate *P. dominulus* differs considerably from that of the tropical *L. flavolineata*. In parti-

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cular, while nests of *L. flavolineata* are active throughout the year and are potentially perennial, those of *P. dominulus* are initiated anew each spring. Established nests of *L. flavolineata* could potentially compensate for reduced group size by recruiting new helpers from a pool of existing pupae. By contrast, unless joiners are available from an external source, foundress groups of *P. dominulus* cannot replace lost nest-mates until their first workers emerge. The colony cycle of *P. dominulus* may thus impose time constraints: it may be easier to preserve the investment of a foundress which dies closer to worker emergence, since any extra effort for the remaining individuals will have to be sustained for a shorter period.

2. MATERIAL AND METHODS

(a) *Natural history of* Polistes dominulus

Polistes dominulus has a colony cycle typical of temperate polistine wasps (Reeve 1991). Nests are initiated in early spring by one or more mated foundresses, with the mean group size in this study being five females (range of 1–19). All foundresses are potentially capable of egg laying (Roseler 1985), but one is behaviourally dominant and lays most or all of the eggs, while her subordinate helpers forage to feed the offspring (Queller *et al.* 2000). In an Italian population, approximately one-third of foundresses were unrelated to their nest-mates (Queller *et al.* 2000). Since insurance-based advantages usually form part of the indirect fitness component (but see Shreeves & Field 2002), only the related majority stand to benefit from them. The first female offspring to reach adulthood mainly become workers, which then rear males and new foundresses that will overwinter. The first workers emerge in late April and May at our study sites. Nest survival rates before worker emergence are low compared with *L. flavolineata*, partly owing to predation of entire *P. dominulus* nests.

At our study site in southern Spain, *P. dominulus* is subject to attack by a social parasite, *P. semenowi*. Before any host workers have emerged, an invading *P. semenowi* female fights the host foundresses and eventually assumes the role of dominant (see Zacchi *et al.* 1996). Remaining host foundresses and subsequent host workers then rear mainly parasite reproductives (see Lorenzi *et al.* 1992).

(b) *Data collection*

Our experiment included *P. dominulus* nests from three nearby sites in southwestern Spain (Conil de la Frontera, Cadiz, 36°15′ N, 06°10′ W; see also Cant & Field 2001). The habitat at each site consisted of pasture or arable fields, with nests occurring on hedges of prickly pear cactus (*Opuntia*). Nests were first initiated during March 1999, when we located a large number of nests. We assigned each nest to be used on one of three removal dates, after blocking for site and attempting to allow for expected nest failures as the season progressed. Because of the high rates of nest failure, however, it was also necessary to locate additional nests prior to the later removal dates, which were randomized with respect to the control or removal treatment.

Prior to each removal date, we ensured that all adult nest-residents were individually marked, and we excluded nests on which *P. semenowi* was already present. We identified dominants as the females most often present on nests during daytime censuses (Cant & Field 2001). We then blocked for total offspring number and group size (1–19 females), and allocated each nest within these blocks randomly to either the removal or control

treatment. We carried out the wasp removals on 1 April (removal 1), 21 April (removal 2) and 28 April (removal 3), by which dates 3%, 50% and 75% of nests contained pupae, respectively. Removals were accomplished by capturing all residents on all nests at dawn, then releasing all except for one to two helpers from each removal treatment nest. We removed the single helper from nests with a group size of two, and two helpers from larger groups.

We mapped the contents of all cells in every nest just before the removals, so that we could subsequently follow the fate of each offspring from weekly brood censuses until the end of May, by which time 97% of surviving nests had produced workers. On each census, each offspring could be assigned to one of three developmental stages: eggs/small larvae, large larvae (which filled the full widths of their cells) or pupae, defined as cells capped with silk.

Reduced groups could potentially preserve investments of their dead nest-mates by recruiting new helpers. Since all nest residents had been individually marked, joiners could be identified as either unmarked foundresses, or foundresses that had previously been marked on another nest. We performed weekly early morning censuses until the end of May to check on the current size and composition of each foundress group. To assess whether the removal treatment altered the foraging effort of the remaining helpers, we used a sample of 46 nests from removal 2. We censused these nests twice in the early afternoon just prior to the removal date (18–21 April), and carried out two similar censuses just after the removals (22–23 April). The proportion of these censuses on which a female is absent from her nest provides an index of her foraging effort (Cant & Field 2001).

AFRs give helpers an advantage over lone foundresses only if most or all of a lone foundress's offspring fail after the death of the foundress (Field *et al.* 2000). A vacant *P. dominulus* nest may be adopted by a foreign female, which may then rear some of the larger offspring to obtain helpers for herself (Nonacs & Reeve 1993, 1995). To test for this possibility in our population, we removed the foundresses from 15 single-foundress nests (four, eight and three nests for removals 1–3, respectively). We checked whether these nests were subsequently adopted by new females, and determined the fate of the original foundress's offspring.

A small number of nests had to be excluded from the analysis owing to nest-mapping ambiguities, leaving totals of 73, 55 and 28 nests for removals 1, 2 and 3, respectively. A total of 88 of these 156 nests survived to produce workers. The remainder were either abandoned or disappeared completely, probably owing to vertebrate predation. Twenty-one nests were taken over by the social parasite *P. semenowi* after the relevant removal date. We include these nests in our analyses, with parasitism as a potential explanatory factor.

(c) *Data analysis*

Just prior to the removals, the total number of offspring increased with group size and date (figure 1). Including the nest with the largest group size (19) suggested that offspring number increased at a decelerating rate with increasing group size ($t = 2.61$ for quadratic term, $p = 0.010$), but without this nest the relationship was linear ($t = 1.811$ for quadratic term, $p = 0.072$). We exclude this nest from subsequent analyses on the grounds of its high leverage, and because it complicates the presentation of results by requiring a quadratic term for group size without altering the main conclusions of the analyses.

Given that offspring number increases with group size, helper removal could cause a reduction in offspring number, to reflect
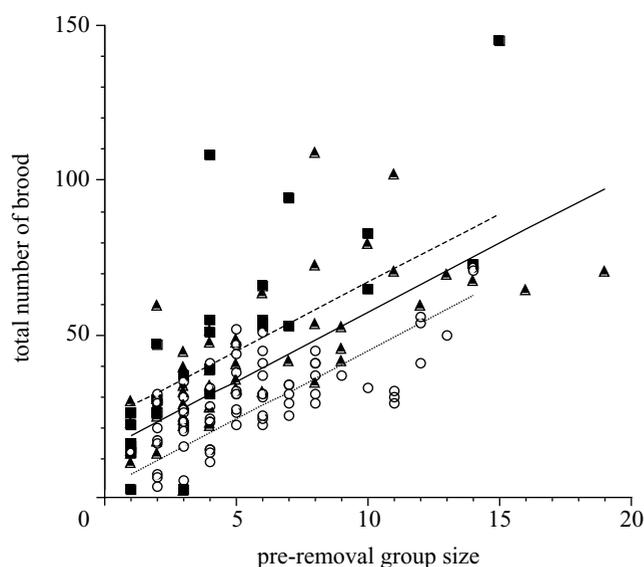
Figure 1. The total number of brood present just prior to helper removals increased linearly with pre-removal group size and also increased from the earliest to the latest removal date: number of brood = 4.60 + 12.4.DATE[2] + 22.2.DATE[3] + 4.44.GROUPSIZE. Standard errors for these estimates are 2.60, 2.65, 3.29 and 0.343, respectively. Lines show the fitted values from this model. Removal 1, open circles and dotted line; removal 2, filled triangles and solid line; removal 3, filled squares and dashed line.
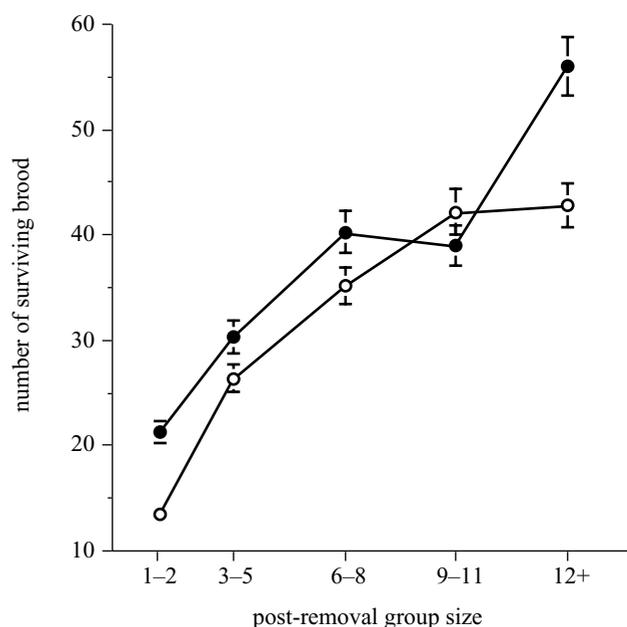

Figure 2. Number of offspring, present at the time of helper removals, that survived until worker emergence. Removal nests had significantly more brood surviving until emergence than would be expected from their post-removal group size: number of surviving brood = 8.96 + 6.55.REMOVAL − 1.21.DATE[2] + 16.0.DATE[3] + 2.88.GROUPSIZE, with standard errors of these estimates being 3.23, 2.68, 2.80, 3.30 and 0.377, respectively. Group sizes are divided into categories so that the trend may be more easily appreciated visually, with bars showing ± s.e. Controls, open circles; removals, filled circles.

the smaller post-removal size of the workforce. If helpers obtain AFRs, however, this does not occur: reduced groups maintain at least some of the 'extra' offspring that they were left with. The date of emergence of the first worker provides a convenient cut-off point at which to assess whether investments have been preserved (see Reeve 1991): after this point, the workforce will increase.

Statistically, the extent of AFRs can be examined using ANCOVA, in which the dependent variable is the number of offspring that survive from the time of the removals until worker emergence, excluding nests that failed before workers emerged. First, if there are AFRs, reduced groups should have significantly more surviving offspring than would be expected from their post-removal group size. Second, if only part of a dead helper's investment is preserved, we expect reduced groups to have significantly fewer surviving offspring than would be expected from their pre-removal group size (Field *et al.* 2000).

Data analysis used general linear modelling with the GLIM statistical package assuming normal, Poisson or binomial error distributions as appropriate (Crawley 1993). In each analysis we first fitted potential explanatory variables (site, group size, treatment, treatment date and whether the nest was subsequently parasitized by *P. semenowi*) and their pairwise interactions. Starting with the interactions, we then subtracted terms from the model until further removals led to significant ($p < 0.05$) increases in deviance. We report significance levels on subtraction for non-significant terms, and on removal from the minimal adequate model for significant terms.

3. RESULTS

(a) *AFRs*

Our results from the 88 experimental nests that survived to produce workers indicate that *P. dominulus* helpers have

AFRs, and that investments of removed helpers are almost completely preserved (figure 2). The total number which survived to worker emergence, of offspring present at the time of helper removals, was higher in reduced groups than would be expected given their post-removal group size ($F = 5.970$, d.f. = 1,79, $p = 0.017$; three nests excluded as they had no brood on the removal date), and not significantly different from expected if group size had not been reduced ($F = 0.52$, d.f. = 1,77, $p = 0.47$). To determine whether small offspring could have been sacrificed to preserve larger ones, we analysed data for large and small brood separately. Simple ANCOVA using post-removal group size as a predictor suggested that larger offspring were preserved ($F = 6.96$, d.f. = 1,79, $p = 0.01$) while small offspring were not ($F = 1.90$, d.f. = 1,79, $p = 0.17$).

Site, or whether a nest became parasitized by *P. semenowi*, had no significant effect on offspring survival ($F = 5.97$, d.f. = 2,76, $p = 0.47$, and $F = 0.48$, d.f. = 1,79, $p = 0.49$, respectively). Treatment date was significant as a main effect ($F = 16.24$, d.f. = 1,79, $p < 0.0001$), with overall offspring survival being higher for removal 3 than removals 1–2, but no two-way interaction terms were significant on successive removal. Thus, the difference between treatments was not affected by treatment date.

Re-adoption of abandoned nests was rare or absent. Thirteen out of the 15 single-female nests that we vacated experimentally remained permanently abandoned, leading to 100% offspring failure. The two remaining nests were subsequently re-occupied, each by a single female. Each

adopting female, however, had originally been marked on the nest concerned but had not been recorded since. It is therefore possible that pre-removal group size had been underestimated for these nests. Neither of these nests ultimately survived to produce workers.

(b) Productivity and development time

The extra large larvae that survived in reduced groups did not cause them to rear fewer offspring in total: of nests that successfully produced workers, reduced groups had the same total offspring number at worker emergence as controls with the same pre-removal group size ($F = 0.04$, d.f. = 1,78, $p = 0.84$ using pre-removal group size in ANCOVA). The number of offspring at worker emergence was significantly higher in reduced groups than expected from their reduced group size ($F = 7.2$, d.f. = 1,84, $p = 0.009$ using post-removal group size in ANCOVA; figure 2). The 'extra' offspring in reduced groups were large rather than small ones: although there was a trend for reduced groups to also have more small offspring, this was not significant ($F = 7.02$, d.f. = 1,82, $p = 0.01$ for larvae + pupae and $F = 3.24$, d.f. = 1,82, $p = 0.076$ for small offspring). Nests used for the last two treatment dates (removals 2–3) had more large offspring at worker emergence than nests in the earliest treatment group (removal 1: $F = 23.78$, d.f. = 1,82, $p < 0.0001$).

The date of first worker emergence did not differ significantly between reduced and control groups ($F = 1.72$, $p = 0.68$), suggesting that offspring did not take longer to develop in reduced groups. Post-removal group size also had no effect on emergence date ($F = 0.36$, $p = 0.55$), but nests parasitized by *P. semenowi* produced their first worker approximately one week before unparasitized nests ($F = 16.83$, $p < 0.0001$). A logistic analysis of whether or not nests became parasitized after their treatment date suggested that parasites were selective in the nests they took over. Take-over rates were lower for smaller groups ($G = 4.337$, d.f. = 1, $p = 0.04$) and for experimentally reduced groups ($G = 6.166$, d.f. = 1, $p = 0.013$). Parasitism rates declined from the first to the last removal date ($G = 25.1$, d.f. = 2, $p < 0.0001$). Probably, this was simply because the later the removal date, the less time before worker emergence, after which *P. semenowi* rarely attacks (Zacchi *et al.* 1996; unpublished data)

(c) Recruitment of new helpers and foraging effort

Overall, 26% of nests that survived to produce workers received one or more joiners after the relevant helper removal date. The mean number of joiners per nest was 0.53 (s.e. of 0.13, range of 0–8). However, experimentally reduced groups were no more likely to receive joiners than controls (logistic ANOVA: $G = 0.83$, d.f. = 1, $p = 0.36$). The percentage of nests receiving joiners declined from the first to the last removal date ($G = 17.1$, d.f. = 2, $p < 0.001$).

We found no evidence that wasps altered their foraging effort after group size reduction: treatment had no effect on the change in foraging effort before versus after the removals ($t = 0.082$, $p = 0.94$).

(d) Nest survival

We could not detect any SI advantage for *P. dominulus* helpers. Overall, 60% (93/156) of nests either succeeded

in producing workers or had not yet produced a worker but were still present at the end of our observations ($n = 5$). Forty-four out of the 63 failed nests were still present but had been abandoned, suggesting that they could have failed owing to the independent deaths of all group members. The remaining 19 nests had disappeared completely, suggesting whole-nest predation. Note that these are underestimates of the overall nest failure rate, as nests that failed before their treatment date were excluded from our analyses.

We carried out a multinomial logit analysis to determine why nests fell into one of three nest-fate categories: nest disappeared, nest abandoned or nest succeeded. The analysis revealed no significant treatment effect on nest fates ($G = 1.01$, d.f. = 2, $p = 0.60$ for the nest fate by treatment interaction). Reduced groups tended to have a higher overall failure rate than controls (31/67 = 46% versus 32/89 = 36%), but this was not significant. There was also no indication that group size had any significant effects, or that the effect of treatment depended on group size. This was true whether group size was considered as a continuous variable ($G = 4.53$, d.f. = 2, $p = 0.10$ for the nest fate by group size interaction) or as categories (1–2, 3–5, 6–8, 9–12, 12+; $G = 10.14$, d.f. = 8, $p = 0.24$). In the latter case, inspection of the standard errors for the group size categories showed that no individual terms were significant. The lack of significance of the complete interaction therefore did not mask any significant effects for smaller group sizes, i.e. those that would be expected to show the largest differences in survival under the SI model (Nonacs 1991). For example, groups of two to three wasps that were reduced to a group size of unity had similar abandonment rates before worker emergence (9/23 abandoned) to non-manipulated controls with group sizes 2–3 (8/19).

Nests that became parasitized by *P. semenowi* were less likely to be abandoned than unparasitized nests ($t = -2.67$, $p = 0.008$), but were no less likely to disappear ($t = 1.16$, $p = 0.25$) or succeed ($t = -0.58$, $p = 0.56$; $G = 11.40$, d.f. = 2, $p = 0.003$ for the complete nest fate by parasitism interaction). Not surprisingly, a later treatment date increased the chance that a nest would succeed ($G = 23.49$, d.f. = 4, $p = 0.0001$ for nest fate by treatment date interaction).

4. DISCUSSION

AFRs occur when offspring that a helper has only part-reared can be brought to adulthood by surviving group members after the helper dies (Gadagkar 1990). Our experiment demonstrates first, that subordinate helpers in foundress groups of *P. dominulus* do benefit from AFRs: reduced groups reared significantly more of their larger offspring than would be expected from their new, smaller group size. Second, AFRs is a factor that benefits helpers but not independent nesters: re-adoption of abandoned nests was at best rare, so that the offspring of lone foundresses were not saved after they died.

By contrast, we were unable to detect a significant SI advantage for helpers in our population. SI operates if larger groups are less likely to fail completely through successive independent deaths of group members (Nonacs 1991; Reeve 1991; Queller 1994; Nonacs & Reeve 1995).

It has previously been suggested that this is the major advantage favouring helping in *Polistes* co-foundress associations (Reeve 1991; Reeve & Nonacs 1997). In a population of *P. dominulus* introduced to North America, Nonacs & Reeve (1995) calculated that SI alone was just enough to favour helping by the first subordinate if co-foundress relatedness was greater than 0.65. In our Spanish *P. dominulus* population, however, there was only a non-significant trend for reduced groups to fail more often than controls, and we could find no significant effects of our removal treatment or of group size on overall nest failure rates. In particular, there was no suggestion that reduced groups with the smallest pre-removal group sizes were especially likely to fail, contrary to expectation under the SI model. There was some random noise in our data owing to probable whole-nest predation: 19/156 nests disappeared completely. Whole-nest predation does not affect the SI model if it acts independently of group size (Reeve 1991), but it does reduce statistical power. We attempted to avoid this by distinguishing nests that disappeared from abandoned nests where group members could have died while foraging, but there remained no significant effect of helper removal, group size or their interaction on abandonment rates. By contrast, we have previously found that an experimental reduction in group size led to a significant increase in group failure rates, consistent with a SI advantage, in the primitively eusocial hover wasp *L. flavolineata* (Shreeves & Field 2002). One possible explanation is that abandonment does not always result from independent deaths in our *P. dominulus* population, but from unknown mortality factors acting on whole groups at the nest.

We have demonstrated that an AFRs advantage operates in two taxonomically and ecologically distinct wasps, *L. flavolineata* (Field *et al.* 2000) and *P. dominulus*. This suggests that AFRs is a mechanism of general importance in primitively eusocial Hymenoptera. We now compare possible mechanisms underlying AFRs in these taxa. In both species, preservation of removed helpers' investments did not come at a cost of slower offspring development, did not lead to correspondingly fewer other offspring being reared, and did not involve increased foraging effort by remaining group members to compensate for the reduced workforce. Compared with the perennial nests of *L. flavolineata*, we expected the annual nesting cycle of *P. dominulus* to impose time-constraints on investment preservation: groups should be less able to sustain rearing extra offspring if nest-mates die long before worker emergence. In fact, we found no effect of treatment date on investment preservation. One caveat is that nests used in removals 2–3 were inevitably self-selected relative to removal 1: nests could not be used if they had failed before a given treatment date. In general, however, this should reinforce the predicted effect of treatment date if surviving nests/wasps tend to be of higher quality. A potential exception might be our exclusion of nests parasitized by *P. semenowi* before a given treatment date. Nests that were parasitized after the treatment produced their first workers significantly earlier, and were less likely to be abandoned, than unparasitized nests. A possible explanation could be that *P. semenowi* preferentially attacks nests of higher quality. Our analyses controlled for the fact that larger nests were more likely to be parasitized after the treatment date,

but *P. semenowi* might assess other aspects of host nest quality that we did not measure. However, since offspring survival was unaffected by social parasitism, it seems unlikely that an effect of treatment date was masked through excluding high-quality pre-parasitized nests from removals 2–3.

One mechanism contributing to investment preservation in *L. flavolineata* is probably the rapid recruitment of replacement helpers. *Listenogaster flavolineata*'s perennial nests usually contain a pool of pre-existing pupae that will soon produce new potential helpers, and reduced groups contain more pupae than expected for their new, smaller group size (Field *et al.* 2000). By contrast, pupae are present during only the last third of the pre-worker phase in the annual *P. dominulus*, so that new recruits must often be obtained from an external source. Recruitment seems unlikely to be a mechanism underlying AFRs in *P. dominulus*, because reduced groups were no more likely to obtain joiners than controls.

An important mechanism underlying AFRs in both *L. flavolineata* and *P. dominulus* is probably the sacrifice of smaller offspring to keep larger, more valuable offspring alive (Field *et al.* 2000). We found in both species that larger offspring were reared through while small offspring were not, and adult *P. dominulus* have been observed to routinely feed eggs and probably small larvae to older larvae (Mead *et al.* 1994). This mechanism for coping with a reduced workforce may be widespread in social wasps because they usually have immature offspring spanning the full age range present simultaneously in their nests, and because each egg or small larva represents only a very small part of the total investment of the group. Wasp larvae are carnivorous, so smaller offspring can readily be fed to larger offspring until either the larger offspring have pupated and no longer require feeding, or until new group members have been recruited. Small offspring may therefore represent a food store that can be used to deal with temporary shortages and can be easily replaced if conditions improve.

A final comparison can be made between primitively eusocial wasps and social vertebrates. No comparable removal experiments appear to have been conducted on cooperatively breeding vertebrates, but Davies (1991) reports that in 11/16 monogamous passerine birds in which both sexes rear the young, male removal during the early nestling period causes a significant decrease in the number of young surviving to fledge. A potential explanation for incomplete AFRs in vertebrates is if they are unable to recycle offspring efficiently: their total brood number is usually smaller, their offspring are of more uniform age, and many species may be unable to make direct use of dead offspring (e.g. Mock & Parker 1997, p. 279). Each offspring therefore represents a relatively large investment, which may be wasted if the offspring is sacrificed. In addition, there is no quiescent pupal stage, so that all offspring require feeding until they are completely independent. A reduction in the adult workforce will therefore have an immediate effect on valuable offspring, and preservation of investments may be possible only through increased foraging effort, which often leads to long-term fitness costs for carers (e.g. Heinsohn & Legge 1999).

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