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Helping effort in primitively eusocial wasps

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In primitively eusocial and cooperatively breeding societies, there is substantial individual variation in helping effort that is not accounted for by variation in genetic relatedness. In primitively eusocial wasps, helpers have a significant chance of inheriting breeding positions. Recent models suggest that because helpers with greater expected future fitness have more to lose, they should invest less in rearing the dominant's offspring. Observations and experiments on the paper wasp *Polistes dominulus* and the hover wasp *Liostenogaster flavolineata* support this prediction: helpers nearer to the front of the queue to inherit dominance, and helpers that stand to inherit larger, more productive groups, work less hard. These findings support the view that variation in social traits is best understood from a life-history perspective. Group augmentation effects, where greater helping effort leads to direct benefits through increased group size, seem less important in wasps. Further studies are required to understand how conflicts over helping effort are resolved in social wasps.

Introduction

An obvious feature of cooperatively breeding and primitively eusocial societies is the substantial variation in individual helping effort. In cooperatively breeding meerkats, for example, the percentage time that individual helpers spend on costly babysitting of the breeders' pups varies from 8% to 42% (Clutton-Brock *et al.* 2000). Similarly, subordinates in paper-wasp co-foundress associations spend between 16% and 94% of their time foraging to feed dependent larvae (Cant & Field 2001). The first attempts to explain this enormous variation focussed on whether helping effort is correlated with genetic relatedness. This possibility has been examined in several cooperatively breeding vertebrates, with positive correlations found in only some species (Clutton-Brock 2002, Canestrani *et al.* 2005). Indeed, a recent meta-analysis showed that on average, only 10% of the variation in helping effort could be explained by variation in relatedness (Griffin & West 2003). There have been few tests of how relatedness influences helping effort in primitively eusocial wasps, and results are again mixed. Among two-foundress associations of *Polistes dominulus* in the laboratory, Queller *et al.* (2000) found a marginally positive correlation between helper-dominant relatedness and the percentage time that the subordinate spent off the nest. However, although time off the nest can be assumed to reflect foraging in field colonies, it is uncertain whether this is the case in laboratory cages. Relatedness was unusually variable in Queller *et al.*'s (2000) Italian field study population. In a Spanish *P. dominulus* population, even when subordinates are sisters of the dominant there is still wide variation in helping effort (Cant & Field 2001; J. Field, C. Bridge, K. Nunn & M. Cant unpubl. data). The third study of helping effort in wasps used the hairy-faced hover wasp *Liostenogaster flavolineata* (Stenogastrinae). In this study, there was considerable variation in relatedness, but relatedness was not correlated with helping effort (Field *et al.* 2006). One caveat with the data from both wasps and vertebrates is that they are only correlative. If relatedness was positively correlated with a third variable that was itself negatively correlated with effort, the true effect of relatedness might be obscured. Second, kin selection could theoretically result in either a positive or negative correlation between effort and relatedness depending, for example, on whether levels of effort are controlled by the dominant or individual helpers themselves (Cant & Field 2001).

Variation in the direct costs of helping

The above results suggest that variation in relatedness is not a general explanation for variation in helping effort. An alternative possibility is that variation in costs and benefits drive helping effort (Heinsohn & Legge 1999). The first indication that this might be the case came from vertebrates. Heinsohn and Cockburn (1994) examined variation in effort put into costly incubation by helpers in the white-winged chough (*Corcorax melamphos*), a cooperatively breeding bird. They found that younger birds incubate less when group size is large. Younger birds lose more weight while incubating, so that incubation is probably more costly for them. The implication was that a large cost is worth paying only when there are large benefits — in small groups when there are few other birds available. Clutton-Brock *et al.* (2000) demonstrated experimentally that costs can influence effort in another cooperatively breeding vertebrate, the meerkat (*Suricata suricatta*). In meerkats, babysitting the dominant's pups is costly for helpers because they are unable to forage while babysitting and so lose weight. Clutton-Brock *et al.* (2000) found that heavier individuals babysit more, and that experimental feeding of helpers led to an increase in babysitting. As in choughs, these results suggest that variation in helping effort partly reflects variation in costs to the helper.

The significance of weight loss in vertebrates depends on how it affects their future survival and reproductive success. A helper might reduce its effort as part of a strategy that maximizes its indirect fitness: the total lifetime effort it can contribute to rearing the dominant's offspring. In addition, however, it may be maximizing its chances of future direct reproduction. In *Polistes*, both subordinate co-foundresses and workers probably have a significant chance of inheriting the position of egg-laying queen (e.g. Queller *et al.* 2000, Cant & Field 2001, Strassmann *et al.* 2004). Recently, Cant and Field (2001, 2005) developed a kin selection model based on the trade-off between a subordinate's helping effort and its future reproductive success. A major prediction of this model is that helpers with greater expected future direct fitness should be prepared to invest less in rearing the dominant's offspring. In many cooperatively breeding vertebrates and primitively eusocial insects, helpers effectively form a temporally stable queue to inherit breeding positions (Field *et al.* 1999, Cant & Field 2001, 2005, Cant & English 2006). Each individual's position in the queue provides an index of its chance of surviving to inherit a breeding position: individuals nearer the front of the queue are more likely to eventually breed. If helpers adjust their levels of effort according to the future fitness they stand to lose, the model predicts that helpers nearer to the front of the queue should work less hard than those further back (*see* Fig. 1). A second general prediction relies on the positive correlation between group size and total productivity that is common in social groups (e.g. Shreeves & Field 2002). If breeders in larger groups are more productive, and if group size remains relatively stable while a helper is queuing, helpers at a given position in the queue should work less hard in larger groups, where they stand to be more productive if they inherit (Cant & Field 2001, 2005). These two predictions hold whether costs of helping take the form of reduced fecundity after becoming a breeder, or reduced survivorship as a helper and therefore a smaller chance of inheritance.

Primitively eusocial wasps such as *Polistes* are ideal systems for measuring the importance of direct costs to helpers, because *Polistes* helpers can reproduce given the opportunity. This is true both of subordinates in co-foundress associations, and of their offspring, known as 'workers'. Even if helpers cannot mate, in haplodiploids they can still lay male eggs. In wasps, foraging is probably the costliest activity performed by helpers because it involves energy-expensive flight and an increased risk of predation away from the safety of the nest (Cant & Field 2001). Cant and Field (2001) found support for their predictions among co-foundress associations of *P. dominulus*: subordinate co-foundresses spent less time foraging if they were closer to inheriting, and if they were in larger groups. However, although order of inheritance has rarely been determined directly, both positive and negative relationships between queue position and effort have been reported in other studies (Cant & Field 2001, 2005, Stiver *et al.* 2005). This probably reflects the correlational nature of these studies: many other variables that could influence the costs and benefits of helping, such as age, size, experience and genetic relatedness, may co-vary with rank, so that causality cannot be assumed. In addition, individuals at position *n* in the queue can occur only in groups of at least size *n*, so that effects of group size and rank may be difficult to disentangle. While there is some support for the prediction that helpers should work less hard in larger groups (Wright 1997, Heinsohn & Legge 1999, Clutton-Brock *et al.* 2000, Cant & Field 2001), it is unclear how much this is driven by future fitness effects. The number of dependent offspring per helper often declines in larger groups, so that an alternative explanation for reduced effort is that there is a smaller payoff from additional help (Michener 1964, Heinsohn & Cockburn 1994, Wright 1997, Heinsohn & Legge 1999, Härdling *et al.* 2003).

In order to demonstrate causality, we would ideally manipulate a helper's expected future fitness. This is difficult in *Polistes* co-foundress associations because we do not know what determines inheritance rank: an individual's position in the queue to inherit. In many other taxa, however, inheritance rank is more or less strictly determined by relative age. The oldest individual is the breeder, and upon her death, the next-oldest inherits her position. An example where such age-based queuing occurs is *Liostenogaster flavolineata* (Fig. 2). *L. flavolineata* is a primitively eusocial wasp in which group size never exceeds 10 females and, in the tropical environment where it lives, brood-rearing continues all year. These features mean that helpers have a relatively good chance of eventually inheriting the sole breeding position in their group (Field *et al.* 1999, Shreeves & Field 2002). Removal of successive *L. flavolineata* dominants revealed that on approximately 90% of occasions, it is the oldest helper that inherits (C. Bridge & J. Field unpubl. data). If the relative ages of the wasps in a group are known, we therefore also know the order in which they will inherit dominance. Field *et al.* (2006) used this knowledge to experimentally manipulate future fitness in *L. flavolineata*. Their first experiment involved removing the Rank 2 females from a set of nests, causing the Rank 3s to be promoted. To control for the reduction in group size, a female below Rank 3 was removed from a further set of con-

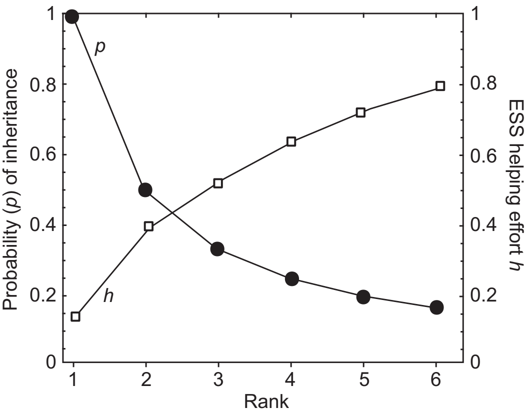

Fig 1. Probability of inheritance (filled circles) and ESS levels of helping effort (open squares) in a social queue. Where group members have equal expected lifespans the probability of inheritance is simply 1/Rank. ESS levels of helping effort are calculated from the model of Cant and Field (2005) assuming that group members are related by coefficient 0.75. In this model, increased helping effort boosts the productivity of the dominant at a cost to the helper's survivorship. The results shown are for a group of size 6. For smaller groups effort levels at each relevant rank are shifted upwards.

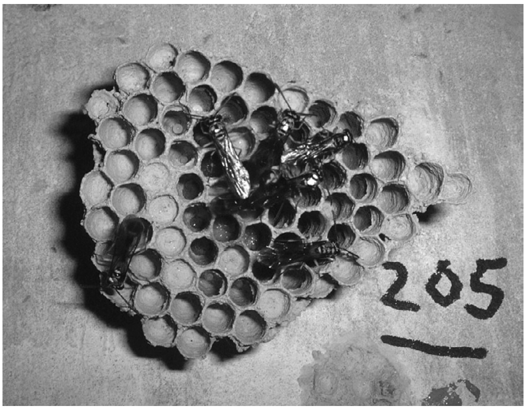

Fig. 2 Mud nest of the hairy-faced hover wasp (*Liostenogaster flavolineata*) with individually marked wasps. Reprinted, with permission, from Nature 11 May 2006, p. vii.

trol nests. On these control nests, focal Rank 3s remained at Rank 3. As predicted by Cant and Field's (2001, 2005) model, promoted Rank 3s spent significantly less time foraging away from the nest after the manipulation than controls (Fig. 3a). One might argue that the laziness of promoted females reflects a necessary function on the nest, perhaps helping to guard against conspecific intrusions. In *L. flavolineata*, however, it is usually the dominant that defends the nest, and defence rarely involves escalated fights (A. Cronin & J. Field unpubl. data). Even if apparently 'lazy' helpers do sometimes defend, the critical question is why it is high-ranking females that do the defending, while low-rankers perform what is likely to be the much costlier task of foraging.

Despite the decrease in group size that they experienced, control Rank 3s did not appear to increase their effort following the manipulation (Fig. 3a) in the way predicted by the future fitness model (Cant & Field 2001, 2005). In the absence of a further control in which group size remained constant, however, it is impossible to draw firm conclusions about the effect of group size *per se*. In order to more rigorously test the effect of group size, Field *et al.* (2006) carried out a second manipulation. This time, the lowest 1–3 ranks were removed from groups of initially 3–5 wasps, leaving only the dominant plus the Rank 2 focal helper. Immature offspring were also removed in proportion to the number of helpers, to ensure that any change in effort by focal Rank 2s was not due to a larger number of

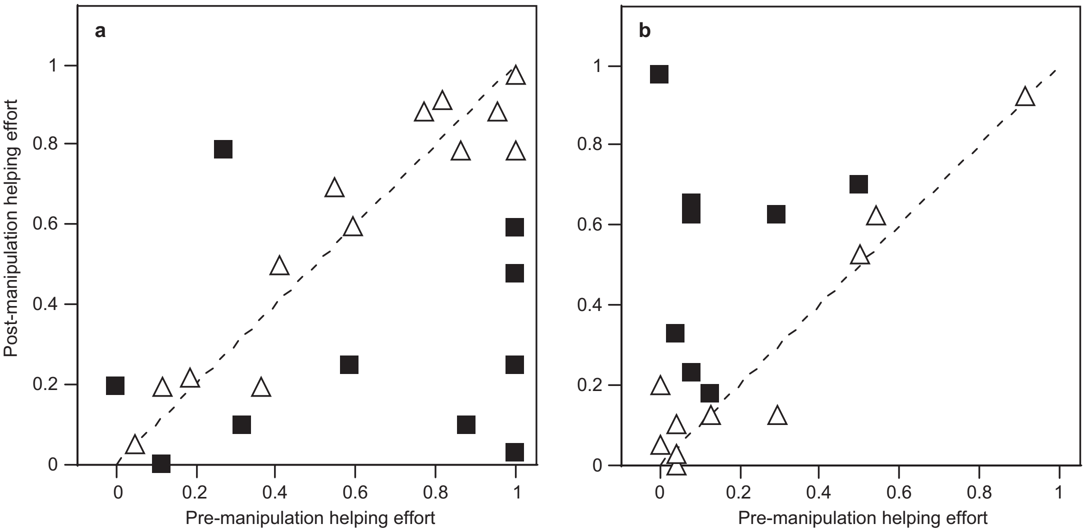

Fig. 3 Effect of manipulating the expected future fitness of *Liostenogaster flavolineata* helpers. In each graph, filled squares are (**a**) focal individuals whose rank or (**b**) group size was manipulated, whereas open triangles are controls. Each data point represents the focal wasp from a different nest. Helping effort was estimated as the proportion of time spent away from the nest. The dashed lines have slope = 1, indicating no change in effort as a result of the manipulations. In both **a** and **b**, treatment and pre-manipulation helping effort have significant ($P \leq 0.01$) effects on post-manipulation helping effort. Redrawn, with permission, from Field *et al.* (2006).

dependent offspring per helper after the manipulation. The result was that focal Rank 2s did increase their helping effort after the manipulation compared with controls (Fig. 3b). This fits with Cant and Field's (2001, 2005) second prediction: focal Rank 2s stood to inherit a smaller group after the manipulation, and were therefore prepared to pay the extra costs associated with working harder. A possible objection to this interpretation is that perhaps the chance of inheritance (from a given rank) is greater in smaller groups, if dominants in smaller groups have shorter lifespans. In *L. flavolineata*, however, experimental reductions in group size caused only a non-significant reduction in dominant lifespan (Shreeves & Field 2002). Furthermore, even if shorter dominant lifespans did increase the chance of inheritance in smaller groups, this would further reduce productivity for the inheriting wasp herself. Overall, Field *et al.*'s (2006) results provide strong evidence that helpers adjust their helping effort according to their expected future direct fitness.

Variation in direct benefits

Where helping reduces survivorship, increased helping effort is costly because it reduces the probability of inheritance and direct reproduction. Some or all of these costs may be offset, however, if the offspring that an individual helps to raise and recruit lead to increased productivity for that individual when it later inherits the breeding position. In wasps, increased productivity could come about either through active helping by offspring (Wiley & Rabenold 1984), or via the passive benefits of increased group size (Kokko *et al.* 2001). Such 'group augmentation' effects can interact with the indirect fitness benefits of helping to produce highly elevated levels of helping effort as compared with those expected from indirect effects alone. Group augmentation benefits could also vary between individual helpers, providing a possible explanation for variation in helping effort. Higher ranked helpers, while more sensitive to the negative impact of helping on the probability of inheritance, are nevertheless more likely to accede to dominant status and reap any group augmentation benefits of helping in the future. Consequently, where group augmentation effects are sufficiently important, higher ranked subordinates are predicted to work harder than lower ranked subordinates (Kokko *et al.* 2001), in direct opposition to the prediction of Cant and Field (2001, 2005).

Polistes co-foundress associations seem a good candidate system for the operation of group augmentation effects. Group productivity increases more or less linearly with co-foundress number (e.g. Shreeves *et al.* 2003), offspring workers actively help, and initial disparities in nest size at worker emergence are likely to be amplified as workers take on the task of nest expansion. Workers do not inherit dominance ahead of subordinate co-foundresses (Hughes *et al.* 1987, Queller *et al.* 1997), so that by rearing the dominant's offspring, subordinates are not creating competitors for themselves. As we have described, however, empirical data offer no support for the predictions of the group augmentation model: higher-ranked subordinates work less hard than lower ranks (Cant & Field 2001). Passive as well as active group augmentation benefits probably operate in *L. flavolineata*, since larger groups are less likely to fail than smaller ones (Shreeves & Field 2002). Even in *L. flavolineata*, however, experimental results give no support to the group augmentation hypothesis (Field *et al.* 2006). While group augmentation may be a major determinant of helping behaviour in cooperatively breeding vertebrates (e.g. Wiley & Rabenold 1984, Clutton-Brock 2000, Clutton-Brock *et al.* 2000), other factors seem to be more important in primitively eusocial wasps.

Discussion

There is a growing consensus that variation in social traits, such as reproductive skew and individual levels of aggression, can be understood only when viewed in a life-history context (e.g. Kokko & Johnstone 1999, Cant *et al.* 2006). The data outlined above support this idea. Individual differences in helping effort in *Polistes* and *Liostenogaster* are not driven primarily by differences in genetic relatedness, but by differences in the direct fitness that helpers stand to lose through working. It is important to note, however, that kin selection is still strongly implicated in the decision to help. In *L. flavolineata*, nest-mates are nearly all relatives, although there is a significant proportion of non-relatives within the Spanish and Italian populations of *P. dominulus* (Queller *et al*. 2000, Field *et al*. 2006, J. Field, C. Bridge, K. Nunn & M. Cant unpubl. data). While females can learn cues associated with natal nest-mates, they seem unable to make the finer distinctions that would be required to distinguish between different classes of relatives (Gamboa 2004). In contrast, future fitness, as reflected by group size and position in the queue, may be easier for individuals to discern. In support of this, Cant *et al*. (2006) showed that in undisturbed *P. dominulus* hierarchies, subordinate aggression was directed primarily towards individuals of adjacent inheritance rank, suggesting that the order of inheritance is known even before any breeding vacancy arises. Precise mechanisms through which individuals assess rank and group size remain unknown.

Data from other social insects tend to support the above conclusions, if it can be assumed that ranks deduced from patterns of aggression are correlated with order of inheritance (references in Ratnieks & Reeve [1992], Cant *et al*. [2006]). It is, however, worth stressing that studies of helping effort in wasps are still in their infancy. Strassmann and Meyer (1983) found that replacement queens among the first generation offspring of *Polistes exclamans* had previously foraged more, rather than less, than lower-ranking helpers. Their study involved only three nests, but suggests that there may be interesting interspecific variation in patterns of effort. If high-ranked helpers tend to be larger, they might be able to afford a higher level of effort, a pattern that probably occurs in some cooperatively breeding vertebrates (Cant & Field 2001, 2005).

While the idea of conflict between carers underlies most models of social caring, how group-members negotiate their levels of effort, and how any 'agreement' is enforced, remains unstudied in wasps (*see* Houston *et al*. 2005 in birds). Negotiation models have been developed to predict the outcome of interactions between two unrelated parents, where each can respond to changes in each other's investment in offspring in real time (MacNamara *et al*. 1999). An important step forward would be to adapt these models to the case of helping behaviour in multimember groups of related helpers, since both relatedness and the number of players are likely to alter evolutionarily stable response rules in the negotiation model. An important empirical challenge in this context is to establish techniques that allow individual levels of effort to be manipulated so that they are perceived as cheating, or as over-working, by other group-members. In addition, while foraging may be the costliest task performed by social insect helpers, performance of other tasks may also be essential for successful brood-rearing: the logic of task apportionment remains unclear. Further investigations of helping effort in primitively eusocial wasps are required to illuminate these issues.

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