

Commentary

Direct fitness, reciprocity and helping: A perspective from primitively eusocial wasps

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In their review, Bergmüller et al. (2007) examine explanations for helping based on direct fitness benefits, and suggest parallels with general cooperation theory. Bergmüller et al. (2007) focus on cooperatively breeding vertebrates. Primitively eusocial wasps, in which all individuals have the option of independent reproduction, comprise the vespid subfamilies Polistinae (paper wasps) and Stenogastrinae (hover wasps), plus the little-studied lineage of apoïd wasps that includes the genus *Microstigmus* (Ross and Matthews, 1991). These wasps have life-histories analogous to cooperatively breeding vertebrates. Indeed, Gadagkar (1994) advocates referring to both groups as ‘eusocial’. In this commentary, we first discuss the evidence that direct benefits drive patterns of helping behaviour in primitively eusocial wasps. We then consider why cooperation theory has rarely been applied to primitively eusocial taxa. Finally, in the light of the limited empirical data, we discuss which mechanisms in Bergmüller et al.’s (2007) classification are likely to be applicable to eusocial taxa.

As Bergmüller et al. (2007) note, three processes through which direct benefits have been thought to influence helping behaviour are known as pay-to-stay, prestige and group augmentation. There are few data with which to evaluate the first two of these as explanations for helping in primitively eusocial wasps. Pay-to-stay is a possibility in that there are significant benefits of group membership, such as resource inheritance, and because independent reproduction often has a low payoff (e.g. Queller, 1996; Field et al., 1999, 2000). However, although helpers are occasionally unrelated to breeders, a substantial fraction of unrelated helpers has been found in only one or two species of *Polistes* paper wasps (Queller et al., 2000; Liebert et al., 2005). In the majority of species, sample sizes available to examine the behaviour of unrelated helpers are therefore small. Since paying-

to-stay should occur principally when relatedness is low (Kokko et al., 2002), the rarity of unrelated helpers in itself suggests that paying-to-stay is unlikely to be common. In *Polistes dominulus*, where ≈35% of foundress pairs are unrelated to each other, Queller et al. (2000) found a marginally significant tendency for helpers to spend more time off laboratory nests when they were more closely related to the breeder. If this pattern also holds under natural conditions, it would suggest that helpers work (forage) harder if they are more closely related to the breeder. Such a pattern might imply that helpers are free to choose their own level of effort (Cant and Field, 2001; Kokko et al., 2002). If they were paying-to-stay, less closely related helpers should be forced to work harder as a payment for any eggs that they lay, and for the chance that they may in future inherit the breeding position. However, different helpers might help for different reasons, and the overall relationship between effort and relatedness could be complex if some helpers pay-to-stay while others help voluntarily (Kokko et al., 2002).

Evidence for paying-to-stay may be difficult to obtain because any payment is likely to be the outcome of a conflict between helper and breeder, and the relative power of the two parties is unclear. In contrast, there is little doubt that group augmentation benefits operate in primitively eusocial wasps. Few studies have compared helper mortality rates in groups of different sizes, but existing data suggest that mortality rates are independent of group size (Shreeves and Field, 2002). Nest predation is also thought to occur independent of group size (Reeve, 1991). However, there is normally a strong positive correlation between group size and breeder productivity (Shreeves and Field, 2002). Furthermore, older individuals typically inherit breeding positions ahead of younger individuals (references in Shreeves and Field, 2002; Bridge and Field, 2007). Thus, if she helps to rear the current breeder’s offspring, an individual will have more helpers herself if she later inherits a breeding position. The importance of these group augmentation benefits will depend on the chance that helpers do later inherit. Inher-

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itance should be more likely in smaller groups, such as hover wasps (Stenogastrinae) and *Polistes* co-foundress associations, where there are fewer competitors for vacant breeding positions (Queller et al., 2000; Shreeves and Field, 2002). Inheritance may be a particularly important component of helper fitness in hover wasps, because brood-rearing occurs all year-round in their relatively aseasonal tropical environments, so that the time available to queue for breeding positions is unconstrained by the arrival of Winter. However, the evidence available suggests that the chance of inheritance itself, rather than the magnitude of group augmentation benefits, drives patterns of helping effort. In both *P. dominulus* and the hairy-faced hover wasp (*Liostenogaster flavolineata*), helpers work less hard when they are nearer to the front of the queue to inherit (Cant and Field, 2001; Field et al., 2006). This is despite the fact that when they are nearer to the front of the queue, helpers are more likely to reap group augmentation benefits through working harder. Thus, while group augmentation presumably is one of the factors that influences helping effort, the major pattern appears to be a reduction in effort by individuals that stand to lose more by working.

Turning now to Bergmüller et al.'s (2007) conclusion that cooperation theory has had little influence on researchers studying cooperative breeding, we note that the same is true of those studying primitive eusociality. In primitively eusocial wasps, one reason is undoubtedly that associations of non-relatives are rare. In most eusocial groups of relatives, individuals appear to gain significant indirect fitness benefits through helping, but it is harder to determine the magnitude of direct benefits, or to separate the influence of direct and indirect benefits on patterns of helping (but see Field et al., 2006). A second reason, discussed by Bergmüller et al. (2007), is that attention has focussed primarily on the choice between becoming a helper and attempting independent reproduction. There is little evidence that individuals switch between the two options depending, for example, on the behaviour of the breeder. In seasonal environments, females that initially choose to become helpers are unlikely to later switch to independent reproduction: the payoff from independent reproduction will generally decline, relative to that of helping to rear the part-grown offspring of a relative, as the time remaining in which to build a new nest and reproduce decreases. Even in relatively aseasonal environments, gradual reduction in a helper's internal resources may reduce the payoff from independent reproduction. How hard a helper works may be regulated by the threat of punishment or eviction, but this has so far been little investigated in primitively eusocial wasps, partly because of the difficulty of manipulating behaviours such as helping. There is, however, evidence of helpers challenging the status of higher-ranked individuals, including breeders, and of occasional role-reversals (e.g. Peters et al., 1995; Field et al., 1998; Seppa et al., 2002; Cant et al., 2006). Eviction could also occur, but is hard to separate from mortality in the field. Challenges are more likely to occur towards the front of the queue for reproductive dominance, and when there is little time left in the season in which to inherit (Cant et al., 2006). Whether challenges can be precipitated by breeder behaviour, however, is unknown.

An additional approach discussed by Bergmüller et al. (2007) that might fruitfully be examined in temperate wasps is market

theory. In *Polistes*, for example, large numbers of foundresses of similar age emerge from hibernation synchronously in Spring and found new nests in groups. Individuals may have the choice of joining several different groups, and switching between groups is not infrequent (e.g. Seppa et al., 2002; Zanette, 2007). Whether switching depends on the strategies of group mates is unknown.

True reciprocity may be rare

Most of the empirical results described above can be explained by mechanisms that do not require individuals to help in expectation of costly return investment by the recipients of that help. In other words, we can explain helping in primitively eusocial wasps without invoking reciprocity. Part of the 'compelling logic' of kin selection (to use Bergmüller et al.'s (2007) phrase) is that realization of benefits does not require costly acts by a recipient in return. The same is true of group augmentation, at least as it might occur in temperate wasps such as *Polistes*. A subordinate wasp may invest in the offspring of the current breeder so that she will have more helpers if she later inherits a breeding position. The workers she helps to create, however, will not usually themselves become breeders, but will help in the future in order to gain kin-selected benefits. This mechanism is therefore an example of pseudoreciprocity—the original investment pays off through the self-interested actions of the recipient. In perennial hover wasps, there at least exists the potential for true cross-generational reciprocity (or 'indirect reciprocity without image scoring' in Bergmüller et al.'s, 2007 terminology) because helped offspring have a chance of becoming breeders themselves: this is a necessary condition if cross-generational reciprocity is to favour helping. But these offspring also have a large kin-selected incentive to help, just as *Polistes* workers do, so that it is unclear how important the benefits due to true reciprocity (rather than pseudoreciprocity) are likely to be. Indeed, the more non-dispersing offspring that are created by the original helper, the lower the chance that any one of these offspring will become a breeder in future, so that the stability of cross-generational reciprocity may be eroded by the very act of helping.

In the case of pay-to-stay, even if in the future we obtain good evidence that wasps help in order to pay 'rent', we believe that this mechanism belongs in the 'pseudoreciprocity' branch of Bergmüller et al.'s (2007) scheme. Pay-to-stay models (e.g. Kokko et al., 2002) assume that in the absence of a costly investment (i.e. help) by a subordinate, the dominant individual, acting out of self-interest, will evict her. This is a clear example of negative pseudoreciprocity, or a 'self-serving punishment' (Cant and Johnstone, 2006). So why do Bergmüller et al. (2007) also allow pay-to-stay as an example of true (negative) reciprocity? They arrive at this conclusion by switching the identity of the actor on the first step: they assume that the dominant makes the initial 'costly investment' by tolerating the subordinate's presence. The subordinate then helps at the second step of the game, in order to avoid expulsion at the third step. Thus we move from negative pseudoreciprocity to negative reciprocity by starting the game one step earlier, namely with the dominant. While these

two alternatives are equally valid theoretically, we think that the former model is more applicable to cooperative breeders. This is because in most cooperatively breeding birds and mammals, and many primitively eusocial wasps, helpers are recruited from within the group. The decision faced by the dominant, therefore, is whether to evict or not, not whether to allow the helper to join. The alternative situation, in which dominants first decide whether to allow a subordinate to join, is relatively rare, although pied kingfishers provide a good example (Reyer, 1984), and perhaps foundress associations in *Polistes* (Reeve, 1991). For most cooperative breeders, and primitively eusocial wasps in particular, the pay-to-stay mechanism will represent an example of negative pseudoreciprocity, rather than negative reciprocity.

Thus, we are left with very few mechanisms relevant to cooperative breeding that depend on true reciprocity, and certainly none for which there is any evidence. The direct fitness mechanisms that have the broadest relevance all belong to the pseudoreciprocity branch of Bergmüller et al.'s (2007) classification. In other words, the most plausible mechanisms, and those for which there is empirical support, do not require individuals to make decisions contingent upon eliciting a costly response from other group members. This is perhaps not surprising: kin selection and pseudoreciprocity are immune to cheating because there is nothing to be gained from non-investment. But it may also reflect the problem that animals face when making decisions in the absence of complete information. In an uncertain world, natural selection can be expected to favour simple 'fail-safe' mechanisms over mechanisms such as reciprocity that are susceptible to unpredictable variation and errors in second-guessing the responses of conspecifics.

In conclusion, models of cooperation have been little utilized in studies of primitively eusocial wasps, and the importance of direct benefits is uncertain. One difficulty is to separate the effects of indirect and direct fitness benefits on patterns of helping: taxa such as *P. dominulus*, in which there is a large proportion of unrelated helpers, may provide a solution. A second difficulty is to manipulate individuals so that they appear to reduce their helping effort but are otherwise unaffected (e.g. Bergmüller and Taborsky, 2005). Finally, as discussed by Bergmüller et al. (2007), models of cooperation are required that more closely incorporate the biology of primitively eusocial taxa. We believe, however, that reciprocity may be of little importance in cooperatively breeding and eusocial taxa, although further experimental tests are required.

References

Bergmüller, R., Taborsky, M., 2005. Experimental manipulation of helping in a cooperative breeder: helpers 'pay-to-stay' by pre-emptive appeasement. *Anim. Behav.* 69, 19–28.

- Bergmüller, R., Johnstone, R., Russell, A., Bshary, R., 2007. Integrating cooperative breeding into theoretical concepts of cooperation. *Behav. Process.* 76, 61–72.
- Bridge, C., Field, J., 2007. Queuing for dominance: gerontocracy and queue-jumping in the hover wasp *Liostogaster flavolineata*. *Behav. Ecol. Sociobiol.* 61, 1253–1259.
- Cant, M.A., Field, J., 2001. Helping effort and future fitness in cooperative animal societies. *Proc. R. Soc. Lond. B* 268, 1959–1964.
- Cant, M.A., Llop, J.B., Field, J.P., 2006. Individual variation in social aggression and the probability of inheritance: theory and a field test. *Am. Nat.* 167, 837–852.
- Cant, M.A., Johnstone, R.A., 2006. Self-serving punishment and the evolution of cooperation. *J. Evol. Biol.* 19, 1383–1385.
- Field, J., Solis, C.R., Queller, D.C., Strassmann, J.E., 1998. Social and genetic structure of paper wasp cofoundress associations: tests of reproductive skew models. *Am. Nat.* 151, 545–563.
- Field, J., Shreeves, G., Sumner, S., 1999. Group size, queuing and helping decisions in facultatively eusocial hover wasps. *Behav. Ecol. Sociobiol.* 45, 378–385.
- Field, J., Shreeves, G., Sumner, S., Casiraghi, M., 2000. Insurance-based advantage to helpers in a tropical hover wasp. *Nature* 404, 869–871.
- Field, J., Cronin, A., Bridge, C., 2006. Future fitness and helping in social queues. *Nature* 441, 214–217.
- Gadagkar, R., 1994. Why the definition of eusociality is not helpful to understand its evolution and what should we do about it. *Oikos* 70, 485–488.
- Kokko, H., Johnstone, R.A., Wright, J., 2002. The evolution of parental and alloparental effort in cooperatively breeding groups: when should helpers pay to stay? *Behav. Ecol.* 13, 291–300.
- Liebert, A.E., Nonacs, P., Wayne, R.K., 2005. Solitary nesting and reproductive success in the paper wasp *Polistes aurifer*. *Behav. Ecol. Sociobiol.* 57, 445–456.
- Peters, J.M., Queller, D.C., Strassmann, J.E., Solis, C.R., 1995. Maternity assignment and queen replacement in a social wasp. *Proc. R. Soc. Lond. B* 260, 7–12.
- Queller, D.C., 1996. The origin and maintenance of eusociality: the advantage of extended parental care. In: Turillazzi, S., West-Eberhard, M.J. (Eds.), *Natural History and Evolution of Paper-wasps*. Oxford University Press, Oxford, pp. 218–234.
- Queller, D.C., Zacchi, F., Cervo, R., Turillazzi, S., Henshaw, M.T., Santorelli, L.A., Strassmann, J.E., 2000. Unrelated helpers in a social insect. *Nature* 405, 784–787.
- Reeve, H.K., 1991. *Polistes*. In: Ross, K.G., Matthews, R.W. (Eds.), *The Social Biology of Wasps*. Cornell University Press, New York, pp. 99–148.
- Reyer, H.-U., 1984. Investment and relatedness: a cost/benefit analysis of breeding and helping in the pied kingfisher (*Ceryle rudis*). *Anim. Behav.* 32, 1163–1178.
- Ross, K.G., Matthews, R.W., 1991. *The Social Biology of Wasps*. Cornell University Press, New York, p. 678.
- Seppa, P., Queller, D.C., Strassmann, J.E., 2002. Reproduction in foundress associations of the social wasp, *Polistes carolina*, conventions, competition, and skew. *Behav. Ecol.* 13, 531–542.
- Shreeves, G., Field, J., 2002. Group size and direct fitness in social queues. *Am. Nat.* 159, 81–95.
- Zanette, L., 2007. Group formation in a social wasp. PhD Thesis, University College London, UK.