

## LETTERS

# Future fitness and helping in social queues

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**Helpers in primitively eusocial and cooperatively breeding animal societies forfeit their own reproduction to rear the offspring of a queen or breeding pair, but may eventually attain breeding status themselves. Kin selection<sup>1</sup> provides a widely accepted theoretical framework for understanding these societies, but differences in genetic relatedness do not explain a universal societal feature: the huge variation between individuals in helping effort<sup>2–10</sup>. An alternative explanation for this variation lies in a fundamental trade-off faced by helpers: by working harder, they increase the indirect component of their fitness, but simultaneously decrease their own future survival and fecundity<sup>2,4,8</sup>. Here, we show that individuals work less hard when they stand to lose more future fitness through working. We experimentally manipulated two components of future fitness in social queues of hover wasps (Stenogastrinae): a helper's chance of inheriting an egg-laying position, and the workforce available to rear her offspring should she inherit. After each manipulation, helpers increased or decreased their effort as appropriate to the change in expected future fitness that they experienced. Although helping provides significant indirect fitness benefits for hover wasps<sup>11</sup>, our study shows that variation in the costs associated with helping is the major determinant of helping effort.**

A conspicuous general feature of primitively eusocial and cooperatively breeding societies is the enormous variation between individuals in helping effort<sup>2–4</sup>. Initial attempts to understand this variation focused on the prediction that more help should be given to closer relatives<sup>5</sup>. Yet tests of this hypothesis have produced mixed results. In eusocial insects, there is little evidence of nepotism within colonies, except when obvious cues like sex of the offspring are correlated with differences in relatedness<sup>6,7,12</sup>. Kin discrimination is widespread in cooperatively breeding vertebrates, but on average only 10% of the variation in helping effort can be explained by variation in relatedness<sup>5</sup>. This lack of explanatory power has led some to question whether kin selection provides a general explanation for helping<sup>9,10,13</sup>. In this study, we test experimentally whether variation in helping effort is driven primarily by variation in the costs of helping<sup>2–4,8,14</sup>.

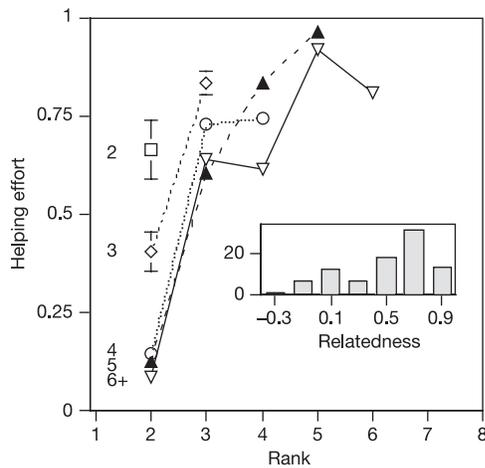
By working harder to rear the offspring of a relative, helpers simultaneously decrease their own future survival and the fecundity they can expect through inheriting breeding positions themselves<sup>2–4,8,15</sup>. This life-history framework suggests that individuals should balance current levels of help against anticipated future fitness returns. Social queues, where group members inherit breeding positions in a predictable, temporally stable order, are widespread in both insects and vertebrates<sup>16–18</sup>. Queues lead to systematic individual variation in future fitness. First, individuals nearer to the front of the queue have a shorter wait to inherit, and therefore a greater chance of surviving to breed<sup>14,8,16,17</sup>. Second, if breeders are more productive in larger groups, individuals waiting in longer queues can expect greater reproductive success should they succeed in inheriting breeding positions<sup>4,8,16</sup>. If non-breeders adjust their helping effort according to their expected future fitness, we can make

two predictions. First, high-ranking individuals should work less hard than low-rankers. Second, individuals at a given rank in the queue should work less hard in larger groups. In both cases, individuals work less hard when they expect to lose more future fitness through working. We test these predictions experimentally in the tropical hairy-faced hover wasp *Liostenogaster flavolineata* Cameron, a system in which both rank and group size can be manipulated.

*L. flavolineata* (Hymenoptera: Stenogastrinae) nests in groups of 1–10 related<sup>19</sup> females (within-nest coefficient of relatedness in this study  $r = 0.46 \pm 0.08$ ). A single female, known as the dominant or rank 1, lays almost all of the eggs and rarely leaves the nest<sup>19</sup>. She is morphologically undifferentiated<sup>20</sup> from other group members, known as helpers (rank 2 and upwards). Helpers provide aid by foraging to collect food for the dominant's immature larvae, and helping effort is conveniently measured by time spent away from the nest<sup>4</sup>. Number of offspring reared is positively correlated with group size<sup>11,16</sup>, so that helping provides indirect fitness benefits. Dominance in *L. flavolineata* is determined through strict age-based queuing, with rank 1 being the oldest female. When rank 1 dies or is experimentally removed, the next-oldest female becomes dominant in 90% of cases<sup>21</sup>. By knowing their relative ages, it is thus possible to order females precisely according to their positions in the queue. Reduced helping effort by high-ranking females could be adaptive, because females reaching rank 1 experience a significant increase in expected lifespan<sup>16,18</sup> and rear offspring to which they are more closely related<sup>11</sup>.

Consistent with our predictions based on future fitness, in unmanipulated *L. flavolineata* groups, lower-ranked helpers and helpers in smaller groups worked harder (Fig. 1 and see Methods). As in other systems<sup>9</sup>, a helper's genetic relatedness to the dominant egg layer had no effect on her helping effort, despite considerable variation in relatedness (Fig. 1 inset). In order to test whether future fitness determines helping effort causally, we experimentally manipulated two components of the direct reproduction that a helper could expect in the future. In experiment 1, we tested whether chance of inheritance determines helping effort by experimentally promoting females that lay third in the queue (Fig. 2a). We removed the second-oldest (rank 2) female from each experimental group, so that focal rank 3 helpers were promoted to rank 2. We controlled for the resulting change in group size by removing a low-ranking female (below rank 3) from a second set of matched groups. As predicted, experimental rank 3 helpers, whose chance of inheriting had been increased by the manipulation, afterwards worked significantly less hard than control rank 3 helpers, whose chance of inheriting remained unchanged (Fig. 3a). Before being promoted, experimental rank 3 helpers had worked significantly harder than control rank 2 helpers ( $62 \pm 13\%$ ,  $n = 10$  versus  $11 \pm 3\%$ ,  $n = 13$  time off the nest,  $P = 0.002$ ). After being promoted to rank 2 themselves, however, experimental rank 3 helpers worked approximately as hard as control rank 2 helpers ( $27 \pm 8\%$  versus  $20 \pm 6\%$ ,  $P = 0.5$ ). Our manipulation altered the relationship between helping effort and age, in

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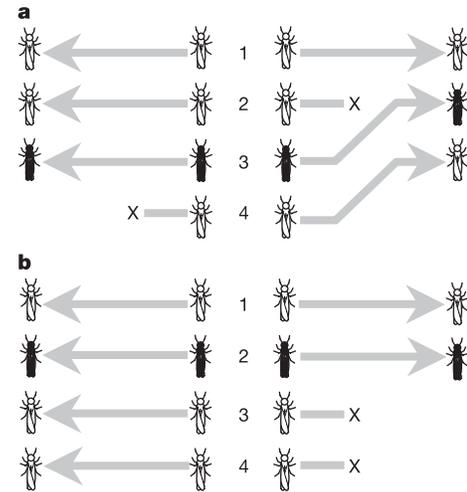


**Figure 1 | Helping effort as a function of rank and group size in unmanipulated *L. flavolineata* groups.** Each line represents a different group size, as indicated by the numbers on the left of the graph (open square, 2; open diamond, 3; open circle, 4; filled triangle, 5; open triangle, 6+). Helping effort is estimated as the proportion of censuses spent away from the nest. For clarity,  $\pm$ s.e.m. is shown for only the two smallest group sizes, which include the largest and smallest errors. In an analysis of covariance using the full data set of 332 helpers (97 nests), helper rank, group size and helper absolute age had significant ( $P < 0.0001$ ) effects on effort, together accounting for 45% of the total variation. The effect of absolute age was that younger helpers worked harder. Helper-dominant relatedness had no effect ( $P > 0.5$ ) when the analysis was repeated using a subset of 88 helpers from 2001 for which genotypes were available. Inset gives the frequency distribution of the 88 helper-dominant raw relatedness values, showing peaks close to the expected values for cousins ( $r = 0.1875$ ) and sisters ( $r = 0.75$ ). See Methods for further details.

which younger (lower-ranked) helpers normally work harder than older (higher-ranked) helpers. Despite being significantly younger than control rank 2 helpers ( $55 \pm 13$  days old versus  $116 \pm 10$  days old,  $P = 0.001$ ), promoted rank 3 helpers still behaved as expected for their new rank, suggesting that rank itself, rather than age or any other correlate, has a causal effect.

In experiment 2, we tested the response of rank 2 helpers to a second component of future fitness: the workforce available to rear their offspring should they succeed in inheriting. We experimentally reduced the workforce by removing all but ranks 1 and 2 from groups where there were initially 3–5 females (Fig. 2b). In order to avoid leaving reduced groups with more dependent offspring per helper than unmanipulated controls<sup>11</sup>, we also removed a proportion,  $R/N$ , of the immature larvae present on experimental nests, where  $R$  is the number of helpers removed and  $N$  is the initial number of helpers. Although the ratio of helpers/dependent offspring did not differ between treatments after the manipulation, rank 2 helpers on nests where group size had been reduced worked harder than control rank 2 helpers (Fig. 3b). This agrees with our prediction based on future fitness: both sets of rank 2 helpers retained the same chance of inheriting breeding positions, but rank 2 helpers in reduced groups could expect less direct fitness after inheriting because they would have fewer helpers. The change in behaviour of experimental rank 2 helpers is unlikely to represent an abnormal response to disturbance caused by the manipulation. We allowed a 2-day gap between the manipulation and measurement of post-manipulation helping effort. Also, after their groups had been reduced, experimental rank 2 helpers spent a similar proportion of time off the nest ( $54 \pm 10\%$ ,  $n = 8$ ) as rank 2 helpers in unmanipulated groups of two females ( $47 \pm 9\%$ ,  $n = 7$ ).

Our results suggest that the trade-off between current levels of help and future direct fitness through inheritance is a major determinant of helping effort in *L. flavolineata*. Helpers can respond to

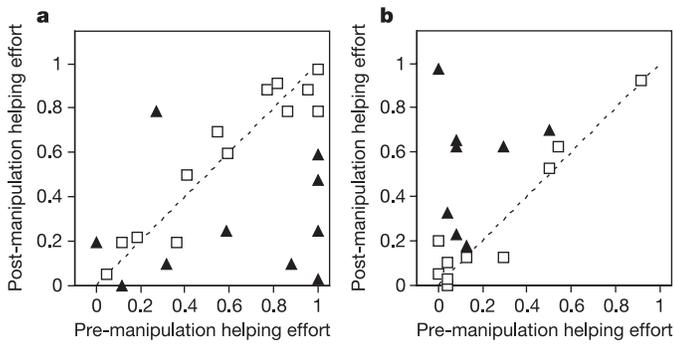


**Figure 2 | Experimental design with a group size of 4 females.** Numbers indicate ranks (rank 1 is the dominant). The right-hand side of each figure represents nests where the rank (experiment 1; **a**) or group size (experiment 2; **b**) of the focal wasp (in black) was manipulated, whereas the left-hand side represents control nests. On each side, the inner column of 4 wasps shows the pre-manipulation state and the outer column the post-manipulation state, where crosses signify individuals that were removed in the manipulations. Note that experiment 1 can be used to draw conclusions about the effect of rank but not group size, as group size was manipulated to the same extent in both treatments.

changes in their position in the queue or the size of their group by either increasing or decreasing their effort as appropriate. Our results imply that two other processes that could modify helping effort—group augmentation and compensation—are less important in *L. flavolineata*. Group augmentation occurs when an individual can boost group size by helping, so that she will later have more helpers herself if she survives to inherit<sup>22</sup>. However, group augmentation effects should have led to the rank-promoted females in experiment 1 working harder rather than less hard, because the manipulation increased their chance of inheriting and receiving help from any offspring that they contributed to rearing. Our result suggests that such benefits are outweighed by the negative effect that working harder would have on the chance of inheritance itself.

*L. flavolineata* helpers respond differently to changes in how hard other group members work compared with birds, where the removal of helpers causes remaining adults to compensate by increasing their own helping effort<sup>23</sup>. In experiment 1, compensation would have required both control and experimental rank 3 helpers to increase their effort in response to the larger number of dependent offspring per helper after the manipulation. Instead, the control groups showed no compensation, and the experimental groups decreased their effort (Fig. 3a). A key difference may be that clutch size cannot easily be adjusted in many birds, so that the death of a helper increases the benefits of additional help for remaining individuals. In contrast, wasps can respond to helper removals by recycling excess offspring: older excess offspring left after the death of a helper are probably reared by feeding smaller offspring to them, so that investment can be preserved without increasing foraging<sup>11,24</sup>.

Variation in effort among *L. flavolineata* helpers is a response to variation in the cost parameter ( $c$ ) in Hamilton's rule<sup>1</sup> ( $rb > c$ ). Although helpers clearly gain indirect fitness benefits through aiding natal nest-mates, informational constraints<sup>6</sup> may prevent them from responding to variation in relatedness within the group. In contrast, rank and group size may provide easily discernible indications of the future fitness that a helper stands to lose, allowing levels of effort to be behaviourally fine-tuned. Rank and group size should influence an individual's propensity to perform any action that jeopardizes its future fitness, and should be part of any



**Figure 3 | Results from manipulating the expected future fitness of *L. flavolineata* helpers.** In each graph, filled triangles are focal individuals whose rank (experiment 1; **a**) or group size (experiment 2; **b**) was manipulated, whereas open squares are controls. Each data point represents the focal wasp from a different nest. The dashed lines have slope = 1, indicating no change in effort as a result of the manipulations. **a**, In experiment 1, both treatment ( $P = 0.01$ ) and pre-manipulation helping effort ( $P = 0.01$ ) had significant effects on post-manipulation helping effort ( $n = 23$ ). There was also a significant interaction between treatment and pre-manipulation helping effort ( $P = 0.003$ ): focal rank 3 helpers that were already making little effort before the manipulation could not decrease their effort much further after the manipulation. **b**, In experiment 2, both treatment ( $P = 0.003$ ) and pre-manipulation helping effort ( $P = 0.002$ ) had significant effects on post-manipulation helping effort ( $n = 18$ ).

framework for understanding patterns of individual behaviour in social hierarchies<sup>8</sup>.

## METHODS

Each experiment used nests situated in culverts (sites) that carried streams under a 4-km stretch of road surrounded by forest between Raub and Bukit Fraser in Pahang State, peninsular Malaysia<sup>11,16</sup>. Experiment 1 was conducted in late August 2001 and experiment 2 in late August 2003. The relative ages of wasps within each group were known as a result of intensive monitoring for the 5 months before each experiment, during which each newly emerged female was individually marked soon after she reached adulthood<sup>18</sup>. In groups where the relative age of the two oldest females was unknown because they had both been present from the start of monitoring, the rank 1 could be identified behaviourally<sup>18,20</sup>. We allocated nests randomly to treatments after blocking for site, total number of immature offspring and group size (4–8 females in experiment 1; 3–5 females in experiment 2).

Each experiment consisted of three phases. First, all nests were censused every 30 min during the main foraging periods (7.00–11.00) on three consecutive days (days 1–3), for a total of 22 (experiment 1) or 24 (experiment 2) censuses. Each individual's pre-manipulation helping effort was estimated as the proportion of censuses on which she was away from the nest. The second phase was the manipulation itself, carried out on day 4 (experiment 1) or day 6 (experiment 2). All residents on all nests were captured before dawn; subsequently all were released except for the helpers to be removed. In experiment 2, we removed immature offspring from experimental nests at the same time as removing adults. Offspring were divided into three categories: eggs/tiny larvae, medium larvae and large larvae. A proportion,  $R/N$ , of each category was removed using a pooter. Pupae, which do not require feeding, were not removed. The final phase of each experiment was estimation of post-manipulation helping effort, on consecutive days 7–10 (experiment 1) and 8–12 (experiment 2), using half-hourly censuses as before. A few groups had to be omitted from the final analysis because group size changed naturally during the course of the experiment or the focal female died or moved up in rank naturally.

**Statistical analyses.** Data were analysed using generalized linear modelling in the R statistical package (version 2.0.0 for Macintosh)<sup>25</sup>. The data in Fig. 3 were analysed with  $y$  = the focal female's post-manipulation helping effort (that is, her proportion of censuses off the nest). Explanatory variables tested were treatment and the focal female's pre-manipulation helping effort. In the analysis of Fig. 1, explanatory variables tested were helper rank, group size, site, number of immature offspring, helper wing length, helper absolute age and year (2001 or 2003). Rank was correlated with group size ( $r^2 = 0.32$ ; individuals at position  $n$  in the queue can occur only in groups of at least size  $n$ ) and with absolute age ( $r^2 = 0.33$ ; higher-ranked individuals tend to be older). We included all helpers

for which data were available for all explanatory variables ( $n = 169$  helpers from 47 nests in 2001;  $n = 163$  helpers from 50 nests in 2003; these included the nests that were subsequently manipulated). The same variables had significant effects when data from each year were analysed separately. The effect of relatedness was tested using a subset of 88 of the helpers from 2001. Relatedness was estimated from genotypes at three hyper-variable microsatellite loci (loci and methods as described previously<sup>19</sup>). Relatedness had no significant effect whether it was coded as a raw value; a binary variable where 1 = helper significantly ( $P < 0.05$ ) more likely to be a sister than a cousin of the dominant ( $n = 48$  individuals) and 0 = this was not the case ( $n = 40$ ); or a binary variable where 1 = helper significantly ( $P < 0.05$ ) more likely to be a sister than a niece of the dominant ( $n = 35$ ) and 0 = this was not the case ( $n = 53$ ). Raw values were estimated using the computer program Relatedness version 5.08 (<http://www.gsoftnet.us/GSoft.html>)<sup>26</sup>. Tests of sister–cousin and sister–niece relationships were conducted using the computer program Kinship version 1.3.1 (<http://www.gsoftnet.us/GSoft.html>)<sup>27</sup> with a power of 93% (sister–cousin) or 76% (sister–niece) at the  $\alpha = 0.05$  level.

We began all analyses with all explanatory variables fitted. Starting with interaction terms, we then subtracted terms from the model until further removals led to significant ( $P < 0.05$ ) increases in deviance, as assessed from tabulated values of  $F$  with normal errors or  $\chi^2$  with binomial errors<sup>28</sup>. We report significance levels for terms when adding them last to this minimal adequate model. When there was significant overdispersion using binomial errors, we re-fitted the model assuming a quasibinomial error structure<sup>25,28</sup>. In each statistical analysis where the dependent variable was helping effort (proportion of censuses spent away from the nest), the results were quantitatively almost identical whether the error structure assumed was binomial or the dependent variable was arcsine-square root transformed then normal errors assumed. Means  $\pm$  standard errors are reported.

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