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**Insurance-based advantage to helpers in a tropical hover wasp**

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The origin and maintenance of eusociality is a central problem in evolutionary biology<sup>1,2</sup>. Eusocial groups contain individuals that forfeit their own reproduction in order to help others reproduce. In facultatively eusocial taxa, offspring can choose whether to found new nests or become helpers in their natal groups. In many facultatively eusocial insects, offspring need continuous care during development, but adult carers have life expectancies shorter than the developmental period<sup>3–7</sup>. When a lone foundress dies, her partly reared brood are usually doomed. Here, we show that helpers in a tropical hover wasp (*Liostenogaster flavolineata*) have an insurance-based advantage over lone foundresses because after a helper dies, most of the brood that she has partly reared will be brought to maturity by surviving nest-mates. After some of the helpers are experimentally removed from a multi-female nest, the reduced group is left with more brood than it would normally rear. We found that larger, more valuable extra brood were reared through to maturity, but not smaller, less valuable brood. Smaller brood may be sacrificed to feed larger brood, and reduced groups probably benefited from increased short-term helper recruitment. Rearing extra brood did not increase adult mortality or brood development time.

The life histories of many facultatively eusocial insects are characterized by a long period of offspring dependency in relation to a short life expectancy for adult carers<sup>3–7</sup>. A lone foundress must carry out risky foraging to feed her brood, but will obtain zero reproductive success unless she survives the entire offspring development period. Among 19 species of polistine wasp, 38–100% of nests of lone foundresses fail before any adult offspring emerge<sup>3</sup>. Instead of founding a new nest, a female may choose to help a dominant relative. Although a helper will still have to carry out risky tasks, insurance-based mechanisms can potentially preserve some or all of her investment if she dies, giving her an advantage over lone foundresses<sup>3–8</sup>.

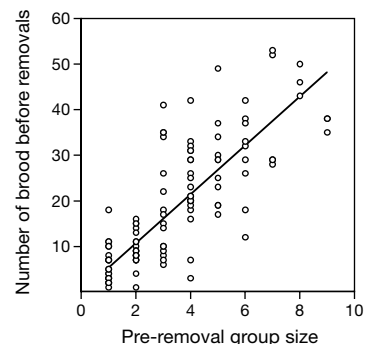
The most conceptually straightforward of these advantages has been termed assured fitness returns<sup>5</sup> (AFRs). The idea is that even if

a helper lives for only a few days, the offspring that she part-rears can subsequently be brought to adulthood by surviving group members<sup>5,7</sup>. Calculations indicate that this mechanism would often favour helping at helper–brood relatedness thresholds as low as 0.1 (ref. 5). These calculations, however, make an important untested assumption: the reduced workforce remaining after a helper's death must somehow continue to rear the extra brood contributed by the helper in addition to the brood that a smaller group would normally rear. Here, we test this assumption experimentally.

Hover wasps (Stenogastrinae) comprise around 50 species found in southeast Asian/Papuan rainforests<sup>9,10</sup>. *L. flavolineata*<sup>10–13</sup> builds small mud nests (up to 90 cells) initiated by single foundresses in moist, protected places such as under bridges or rocks overhanging water. Large aggregations of nests form at some sites. The number of residents on a nest is relatively small (less than 10 females) and there are no morphological castes<sup>10,11</sup>. Newly emerged adult females may either disperse or become helpers which defend their natal nests and forage to feed the brood<sup>10,12</sup>. Brood rearing and nest founding occur throughout the year at our study sites in Malaysia, with no fixed end to the colony cycle. Genetic work using microsatellites indicates that female nest-mates are close relatives (coefficient of relatedness  $r = 0.52 \pm 0.05$ ) and that one dominant female lays almost all of the eggs (S.S., M.C. & J.F., unpublished data).

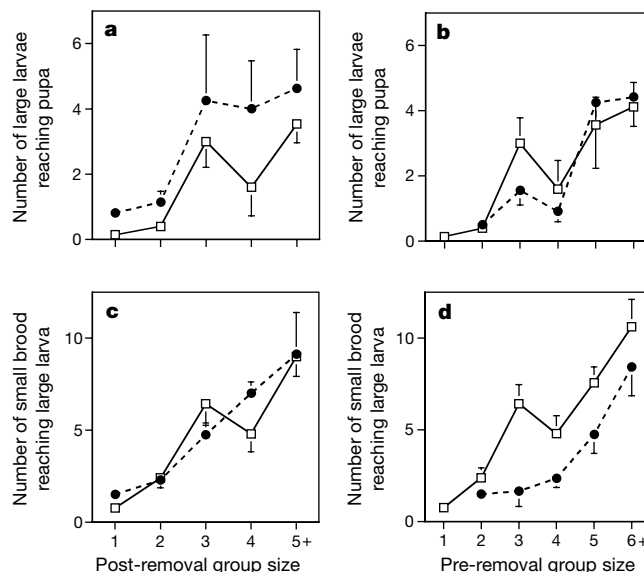
Insurance-based advantages are likely to be important in *L. flavolineata*<sup>13</sup>. Eggs take about 100 days to reach adulthood<sup>10</sup>, but only 10–30% of lone foundresses can expect to survive that long<sup>13</sup>. To test whether helpers benefit from AFRs, we permanently removed helpers from each of 46 multi-female nests: we removed a single helper from each of 10 two-female nests, and two helpers from all other nests. Another 45 multi-female and 21 lone-female nests acted as controls. We distinguished two size classes of non-pupal brood. Of these, 15% were large larvae (mean weight  $51.6 \pm 3.7$  mg), which take about 3 weeks to reach the pupal stage, and 85% were small brood (eggs or small larvae:  $0.81 \pm 0.05$  mg), which take about 7 weeks.

At the time of helper removals, there was a positive linear relationship between group size and the number of each offspring stage being reared (Fig. 1 shows total brood). Removing two helpers from groups of  $n$  wasps therefore left the remaining  $n - 2$  wasps with more brood to rear than their post-removal controls (unmanipulated groups with the same post-removal group size of  $n - 2$ ). The extra brood represent part of the investment of the two dead helpers. If reduced groups reared no more brood through to maturity than post-removal controls, none of this investment would be preserved and there would be no AFRs advantage to helpers. At the opposite extreme, if reduced groups reared as many brood through to maturity as their pre-removal controls (unmanipulated groups with the same pre-removal group size of  $n$ ), then the dead helpers' investment would be completely preserved.



**Figure 1** Number of brood in relation to group size just before removals. Equation of line is Brood =  $5.36 \times$  Group size,  $r = 0.79$ ,  $P < 0.0001$ . Adding a quadratic term or a non-zero intercept did not significantly improve the fit of the model.

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**Figure 2** Relationship between group size and the number of brood present just before the removals that were reared to the next developmental stage on control (open squares) and removal (filled circles) nests. **a, c**, Post-removal group size; **b, d**, pre-removal group size. Treatment is significant in **a** ( $P = 0.003$ ) and **d** ( $P < 0.0001$ ). There is also a significant site–treatment interaction (not shown) in **c** ( $P = 0.0007$ ) and **d** ( $P = 0.004$ ).

If this interaction is not fitted, site ( $P = 0.0002$ ) but not treatment ( $P = 0.21$ ) remains significant in **c**, whereas both site ( $P = 0.02$ ) and treatment ( $P < 0.0001$ ) remain significant in **d**. Site is also significant in **a** and **b**:  $P < 0.008$ . Group size is significant in all four analyses:  $P < 0.0001$ . Bars show 1 standard error,  $n = 109$  nests.

Our results differed for the two classes of brood. Significantly more large larvae present at the time of the removals were subsequently reared through to the pupal stage by reduced groups than by post-removal controls ( $\chi^2_{(1)} = 9.1$ ,  $P = 0.003$ ; Fig. 2a). Reduced groups reared as many large larvae as pre-removal controls ( $P = 0.51$ ; see Fig. 2b). In contrast, despite starting with  $5.3 \pm 1.7$  more small brood than post-removal controls, reduced groups reared the same number through to the large larval stage ( $P = 0.21$ ; see Fig. 2c), and reared significantly fewer than the pre-removal controls ( $\chi^2_{(1)} = 15.0$ ,  $P = 0.0001$ ; see Fig. 2d). Overall, reduced groups reared the number of large larvae expected if no helpers had been removed, while still rearing the number of small brood expected for their modified group size. As large larvae represent 93% of the total non-pupal brood weight, these results indicate that most of the investment due to the dead helpers was effectively fully preserved. We did not analyse the fate of pupae because their disappearance could represent either failure or hatching. But as pupae do not require feeding<sup>3,14</sup>, results would probably be similar to those for large larvae.

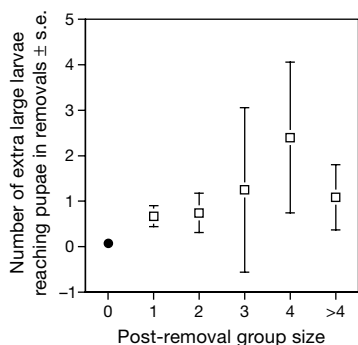
Before concluding that AFRs provide an advantage to helpers, we checked our assumption that when lone females die, they lose their investment in part-reared brood. A vacant nest may be adopted by a new female which may then continue to rear some of the larger brood to obtain helpers for herself<sup>10,13</sup>. If the same number of brood are saved after the death of a lone female as after the death of a helper, then AFRs provide no advantage to helpers. To examine this, we attached 21 vacant nests containing brood among the nests in our main experiment. We found that although 14 of the 21 nests were adopted, less than 1% of the small brood and only 22% of the large larvae were reared through to pupae. Taking into account that natural lone-female nests contained only  $0.33 \pm 0.13$  large larvae, we estimate that when a lone female dies she gets negligible fitness from her partly reared brood (Fig. 3).

Our experiment demonstrates that helpers benefit from AFRs in *L. flavolineata*. Our data suggest three mechanisms by which reduced groups might rear extra brood. First, a few of the large larvae may have been fully fed even before our helper removals. Second, because they were left with approximately 1.4 times as many pupae as post-removal controls ( $\chi^2_{(1)} = 4.3$ ,  $P = 0.04$ ), reduced

groups should have been able to maintain a higher rate of worker recruitment in the short term. The third mechanism relies on the extra small brood that wasps that were left after the removals failed to rear through to large larvae (Fig. 2d). These disappeared completely from nests, and we suspect that they were either eaten by adults or fed directly to developing larvae as occurs in *Polistes*<sup>15,16</sup>. In effect, when faced with extra brood after the death of a nest-mate, the least valuable brood may be sacrificed to bring the most valuable brood to maturity.

We found no evidence that females in reduced groups incurred mortality costs by rearing extra brood. In some avian systems, remaining adults increase their foraging rates after helper removal<sup>17,18</sup>. Whereas the major cost in birds is probably physiological, we would expect increased foraging effort in wasps to incur direct mortality costs<sup>19</sup>. The change in foraging rate (rate after removals minus rate before removals) tended to be more positive in reduced groups than controls, but the difference was not significant ( $P = 0.10$ ). Immediately after the removals, reduced groups did not have higher foraging rates than post-removal controls ( $P = 0.26$ ), nor did they have higher helper mortality rates over the next two months ( $P = 0.65$ ). Treatment had no effect on brood development time after the removals ( $P > 0.19$ ) and the extra large larvae reared by reduced groups did not lead to them rearing correspondingly fewer other brood: two months after the removals, the cumulative total number of brood that had reached the pupal stage remained significantly greater in reduced groups than in post-removal controls ( $\chi^2_{(1)} = 5.19$ ,  $P = 0.023$ ). Group size and brood number remained constant or declined slightly on control nests over the two months, implying that a resource glut did not allow extra brood to be reared.

With the almost complete preservation of a dead helper's investments in *L. flavolineata*, a model developed by Queller<sup>3</sup> shows how a given rate of investment is translated into productivity (offspring) for helpers versus foundresses. The ratio of helper to lone foundress productivity is:  $1/[e^{-qt}(2 - e^{-qt})] = 2.40$ , where  $t$  is brood development time of 100 days (ref. 10) and  $q$  is adult daily mortality rate of 0.0145 (95% confidence interval: 0.012–0.018). The mortality rate is not significantly different for helpers and lone females ( $P = 0.96$ ). Multiplying by  $r_{\text{helper to brood}}/r_{\text{lone female to offspring}} = 0.35/0.5$  (S.S., M.C.



**Figure 3** Number of extra large larvae reared through to the pupal stage on removal nests compared with controls ( $\pm 1$  standard error). The filled circle represents our estimate for lone-foundress nests when the foundress dies.

& J.F., unpublished data) suggests that helping is favoured unless lone foundresses can invest at 1.7 times the rate of helpers. Our data (Fig. 1) suggest that helpers and lone females invest at approximately the same rates.

Insurance-based benefits of helping may be larger in insects than in vertebrates, which have relatively low adult mortality rates<sup>3,4</sup>. Our experiment suggests that an AFRs advantage contributes to the maintenance of helping in *L. flavolineata*. The pattern of investment preservation is obviously adaptive in that it is the older, more valuable extra brood that are reared through to maturity. Additional insurance-based benefits<sup>3,4,6,8</sup> are also likely to operate in *L. flavolineata* and other eusocial<sup>20</sup> and communal<sup>21</sup> insect systems, and similar advantages probably applied at the origin of eusociality<sup>3,6</sup>. □

**Methods**

Our main experiment included all of the active *L. flavolineata* nests in four culverts (sites) that carried streams under a 4-km stretch of road surrounded by forest between Raub and Bukit Fraser in Selangor State, peninsular Malaysia. Starting 17 June 1998, we had individually marked all adult nest residents and identified dominants as the females most often present on nests during regular censuses<sup>11–13</sup>. We allocated nests randomly to removal or control treatments after blocking for site, total brood number and group size (2–9 females)<sup>12</sup>. We carried out wasp removals on 9 July. We captured all residents on all nests before dawn<sup>12</sup>; we then released them all except for 1–2 helpers from each removal nest. By mapping the contents of all cells in every nest just before the removals, we followed the fate of each brood item during subsequent brood censuses every 4–9 days until 9 September. We recognized three brood development stages: eggs/small larvae, large larvae and pupae. We defined large larvae as larvae that filled the full widths of their cells. We focused on whether brood that were initially at one stage successfully reached the next stage. We had to omit a few nests from the analysis because of brood-mapping errors. We calculated mean brood weights from the wet weights of the 324 individual brood in 16 collected nests. Transplanted vacant nests contained  $7.7 \pm 0.3$  brood of all stages, including an average of 1.3 large larvae. Nests were taken without their resident wasps from a site 5 km away and attached<sup>13</sup> among the active nests in our four main sites.

**Data analysis**

We used general linear modelling in the GLIM statistical package assuming Poisson or normal errors as appropriate<sup>22</sup>. In each analysis we first fitted potential explanatory variables (site, group size, treatment) 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, as assessed from tabulated values of  $F$  with normal errors or  $\chi^2$  with Poisson errors<sup>22</sup>. We report significance levels for terms when adding them last to this minimal adequate model. When there was significant overdispersion using Poisson errors, we re-scaled the model using Pearson's  $\chi^2/d.f.$  (where  $d.f.$  is degrees of freedom)<sup>22</sup>. Means  $\pm$  standard errors are reported.

We assumed that foraging effort was proportional to percentage time spent off the nest. To look for possible changes in foraging after the removals, we used the number of wasps off the nest during the foraging periods of 7–8 July versus 12–14 July (9–11 censuses each), excluding data for wasps that were removed. We analysed adult mortality rates using a mark–release–recapture model<sup>12</sup> with data from night censuses every four days until 9 September. For brood development time analyses, the  $y$ -variable for each nest was the number of brood reaching a given developmental stage, with  $\ln(\text{total number of days taken to reach that stage from the previous stage})$  as an offset<sup>22</sup>. We separately examined development times from egg to large larva, large larva to pupa, and pupa to adult emergence. We excluded from the development time analyses any nests that failed or were taken over by foreign wasps between the helper removals and the end of our monitoring. In the analysis of Fig. 2, the same effects remain significant if we exclude nests that failed

between helper removals and the point at which more than 90% of the initial brood stage concerned had reached the next developmental stage. We avoided pseudoreplication by using nests as data points in all analyses except adult mortality.

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**Visual behaviour mediated by retinal projections directed to the auditory pathway**

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**An unresolved issue in cortical development concerns the relative contributions of intrinsic and extrinsic factors to the functional specification of different cortical areas<sup>1–4</sup>. Ferrets in which retinal projections are redirected neonatally to the auditory thalamus<sup>5</sup>**

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