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Ecological constraints on independent nesting in facultatively eusocial hover wasps

Jeremy Field[1], William Foster[2], Gavin Shreeves[1] and Seirian Sumner[1]

[1] *Department of Biology, University College London, Wolfson House, 4 Stephenson Way, London NW1 2HE, UK* (`jeremy.field@ucl.ac.uk`)
[2] *Department of Zoology, University of Cambridge, Downing Street, Cambridge CB2 3EJ, UK* (`wafl@cus.cam.ac.uk`)

Recent field experiments suggest that cooperative breeding in vertebrates can be driven by a shortage of breeding territories. We did analogous experiments on facultatively eusocial hover wasps (Stenogastrinae: *Liostenogaster flavolineata*). We provided nesting opportunities by removing residents from 39 nests within a large aggregation (1995), and by glueing 20 nests obtained from a distant site into a second aggregation (1996). We prevented nest-less floaters from competing for these opportunities in 1995 but not in 1996. In both years, helpers in unmanipulated groups were given opportunities to nest independently without having to incur nest-building costs and with a reduced wait before potential helpers emerged. Helpers visited the nests we provided, but adopted only a small proportion (5% of 111 vacancies created in 1995). Others were adopted by floaters, but a significant proportion of nests were never adopted (9 out of 20 in 1995, 7 out of 20 in 1996). Helpers that visited nests did not originate from particular kinds of social group. Nests containing older broods were more likely to be adopted, and adopting females rarely destroyed older brood. A general feature of social insect, but not vertebrate life histories, namely the long period of offspring dependency relative to the short life expectancy of adult carers, may be a key factor constraining independent nesting.

Keywords: ecological constraints; wasps; eusociality; cooperative breeding

1. INTRODUCTION

Kin selection theory (Hamilton 1964) provides a generally accepted framework for addressing the evolution of altruism, but the relative importance of specific genetic and ecological factors in promoting altruism remains highly controversial. Historically, researchers studying facultative eusociality in insects have been somewhat isolated from those working on 'cooperatively breeding' vertebrates. Insect workers have tended to concentrate on genetic relatedness and the implications of haplodiploidy, whereas vertebrate workers have focused more on ecological factors. Recently, there have been several attempts to integrate these two areas (see, for example, Sherman *et al.* 1995). Of particular interest is the possibility that specific costs and benefits might have the same relative importance in these two major taxa (Brockmann 1997). In cooperatively breeding vertebrates, offspring that 'stay at home' in their natal territories generally do so when resources required for independent breeding are temporarily unavailable or of poor quality compared with those available at home (Emlen 1997). Recent field experiments on three bird species indicate that the limiting resources are high-quality breeding territories: territorial vacancies created experimentally are immediately filled by helpers from existing groups (Pruett-Jones & Lewis 1990; Komdeur 1992; Walters *et al.* 1992). In this paper, we report on analogous experiments done with facultatively eusocial hover wasps (Hymenoptera, Vespidae, Stenogastrinae: *Liostenogaster flavolineata* Cameron).

Hover wasps comprise six genera found in south-east Asian–Papuan rainforests. Their biology is reviewed by Samuel (1987) and Turillazzi (1991). They build small nests (up to about 90 cells in *L. flavolineata*) that are usually initiated by single females in moist, protected places such as caves, or rocks overhanging water. A foundress lays a single egg in each of her first few cells and feeds the resulting larvae progressively on prey she captures. Newly emerged adult females may disperse or become helpers on their natal nests. One female is usually behaviourally dominant on multi-female nests and probably lays most or all of the eggs. Helpers may eventually become dominant on their natal nests.

Hover wasp social groups are small (mean group sizes for populations range from 1–4 wasps), and like social vertebrates there are no morphological castes. Hover wasps live in relatively aseasonal tropical environments in which nesting and nest initiation occur throughout the year (see, for example, Samuel 1987). The absence of a pronounced winter makes it feasible for any newly emerged female to opt for 'delayed' strategies of the sort observed in vertebrates, in which offspring initially become nest-less 'floaters' after dispersing ('disperse and search'), or disperse only when suitable vacancies arise ('stay and foray': Brown 1987). Samuel (1987) found that a large proportion of *L. flavolineata* females do eventually disperse, up to 82 days after emergence. Some dispersers made immediate nesting attempts while others became floaters.

Like other wasps and bees, hover wasps do not defend feeding territories around their nests. The nearest equivalent

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of a vertebrate territory is the nest itself. To reproduce, a dispersing female must find a nest site, build a nest, and rear a brood to adulthood. All three tasks involve significant costs and risks. *L. flavolineata* nests often occur in dense aggregations under overhanging rocks and bridges near streams. In the aggregations we studied, nesting sites do not appear to be limiting: nests are highly aggregated, but there are plenty of suitable spaces in between them. In support of this, there were 23 more nests at our 1996 field site one year after the experiments reported in the next section were done. *L. flavolineata* nests, however, are likely to be unusually costly to build. They are robust, perennial structures constructed entirely of mud, consisting of a single comb of cells plus a thin 'hood' on which wasps sit (Samuel 1987). For comparison, individual cells are approximately 50 times heavier than cells in the flimsy paper nests of *Polistes* (Samuel 1987; J. Field, unpublished data on *P. bellicosus*). At our study sites, more than half of the cells in a typical nest were empty. If she becomes a helper on her natal nest, a female avoids some of the costs of cell-building, as extra brood members can be placed in these empty cells, and cells containing brood are re-used. She also avoids having to find a nest site or build a hood. Nests occasionally become vacant when the owners disappear (Samuel 1987). If independent nesting is constrained primarily by the costs of building a nest, we hypothesize that helpers should leave adjacent social groups and adopt vacant nests, exactly as in the bird studies mentioned (and see Samuel 1987). We report here on the results of creating vacancies experimentally.

2. METHODS

(a) *1995 experiment: bridge site*

In 1995, we used an aggregation of 126 active (brood-containing) nests clustered under a bridge crossing a stream, 30 km north-east of Kuala Lumpur, Malaysia. This is the same aggregation studied by Samuel (1987). The aggregation included another 55 inactive nests, many of which were either mouldy, worn down or being used by other insects. Wasps sometimes sat on these nests for short periods, but they contained no broods.

The nesting area was divided into four areas of 2.5 m × 1.5 m, defined by the four girders of the bridge. Conditions may have been better on girders 1 and 2, where nests had more brood and more residents, and a smaller proportion of nests were inactive (table 1).

All wasps resident on active nests were individually marked during 5–13 July. Periodic night censuses after 13 July allowed further newly emerged wasps to be marked. Daytime censuses and detailed observations on groups of 15–20 nests enabled us to divide residents into three status classes: dominants (one per nest), non-foraging subordinates, and foraging subordinates. Wasps in the first two classes rarely left their nests, but could be separated because dominants laid eggs and were aggressive towards non-foraging subordinates.

The experiment was divided into two parts. In part 1, we removed residents from their nests on 25, 27 and 31 July, but returned them in the evenings so that their brood would be tended on the intervening days. On each removal day, residents were removed before first light by holding a ziplock bag under each nest, causing all wasps to fall in. Then two observers scanned the vacated nests continuously from 0830 to 1730. We were mainly interested in whether wasps from known, pre-existing groups would adopt vacated nests. We therefore prevented competition from known floaters and unmarked wasps by removing them as soon as they landed. A total of 33 nests were vacated on 25 July, with these and an additional six nests being used on the other two dates for a total of 111 day-long vacancies. Vacated nests had broods of 10.2 ± 0.82 members (range 1–23), typical of the nests with one or two residents that occasionally fall vacant naturally. On each bridge girder, a similar proportion of nests (33–38%) was vacated.

Table 1. *Characteristics of nests on the four bridge site girders prior to the 1995 experiment, and before 18 nests were colonized by ants*

(Probabilities are for comparisons between the four girders using *G*-tests (proportion of nests inactive) or *F*-tests (group size, ln[no. brood]).)

girder	no. active (inactive) nests	active nests: group size	active nests: no. of brood
1	21 (5)	3.33 ± 0.48	20.4 ± 2.88
2	36 (5)	3.77 ± 0.35	19.0 ± 1.87
3	12 (7)	2.42 ± 0.42	12.6 ± 2.78
4	57 (38)	2.86 ± 0.21	13.6 ± 1.05
	$p<0.005$	$p<0.1$	$p\approx0.1$

In part 2 of the experiment, residents were returned to only 19 of the vacated nests on the evening of 31 July. Residents from the remaining 20 nests were killed, then their nests were censused every other day until 11 August. This allowed us to detect further adoptions, and to check whether wasps that had moved to these nests during 31 July would stay permanently.

Ants had colonized a cluster of 18 active nests on girder 4 immediately before our experiments began—the only time that this occurred. Further infestation was prevented by surrounding the cluster with grease. The 59 former residents of these nests provided us with a known pool of marked floaters.

(b) *1996 experiment: gazebo site*

In 1996, we did a similar experiment using an aggregation of 80 active and four inactive nests under a circular summerhouse 10 km north of the 1995 site (see Turillazzi 1990). All residents were marked during July–August. Group sizes (3.16 ± 0.18, range 1–7) were similar to those at the 1995 site (3.11 ± 0.17, range 1–10), and the status of residents was determined as in 1995.

In 1996, vacancies were created by adding broods of new nests to the aggregation. On 31 August, 20 nests containing broods of 11.3 ± 1.74 members were collected without their residents from a site 40 km away. These nests were glued onto the summerhouse at 0600 on 1 September, spread evenly among the nests already present. The added nests were censused every 30–60 min from 0600–1830 on 1–2 September, then once every other night until 11 September. The nests were then removed and the experiment terminated. Unlike 1995, floaters were not prevented from adopting vacant nests.

(c) *Statistics*

Data were analysed using GLIM. In each analysis, all explanatory variables and interactions were fitted simultaneously, then terms were removed following the procedure recommended by Crawley (1993, p. 189) until further removals led to significant ($p=0.05$) increases in deviance, as determined from *F*-ratios for

Table 2. *Wasps recorded on vacated nests during the 1995 experiment*

(The 272 nest residents were from 69 unmanipulated nests. We could not tell which of two non-foragers was the dominant on 13 nests: these 26 wasps are classified as non-foragers.)

status	number in aggregation	percentage recorded on vacated nests, 25 July–11 August	percentage permanently adopting vacated nests, 25 July–11 August
lone females	6	33.3	0
dominants on multi-female nests	50	2.0	0
non-foragers	39	17.9	10.3
foragers	177	14.7	3.4
total nest residents	272	13.2	3.7
floaters from nests colonized by ants	59	44.1	?[a]
other floaters	?	25 wasps	?[a]

[a] Unknown because floaters were removed when they landed on vacated nests.

Table 3. *Effect of nest position and oldest brood stage on the proportion of days on which vacated nests attracted nest residents and floaters in part 1 of the 1995 experiment*

	nest position		oldest brood	
wasp status	girders 1–2 (20 nests)	girders 3–4 (19 nests)	pupae (16 nests)	eggs/larvae (23 nests)
nest residents	0.40[b]	0.13[b]	0.43[a]	0.16[a]
floaters	0.41	0.40	0.40	0.41

[a] Oldest brood: $p < 0.025$.
[b] Nest position: $p < 0.005$.

normal errors or χ^2 tables for binomial or Poisson errors. We report significance levels for removal of further terms from this minimal adequate model. We quote estimates ± s.e.

3. RESULTS

(a) *1995: bridge site*

During part 1 of the experiment, 28 (10%) of the 272 residents remaining on unmanipulated nests were seen visiting one or more of the vacated nests. However, most visits were only temporary and only six visitors were still present at the end of the day on which they visited, representing only 5% of the 111 day-long vacancies. There was no evidence that temporary visitors stole or consumed brood from nests they visited, and they subsequently returned to their original nests.

In part 2 of the experiment, 11 (55%) out of 20 permanently vacated nests were permanently adopted, six by residents from unmanipulated nests and five by floaters. The other nine (45%) nests were never adopted. The adopting wasps included all four females that were still on vacant nests by the end of part 1 of the experiment on 31 July.

We used analysis of covariance (Crawley 1993) to determine whether the tendency for nest residents to visit vacant nests depended on their age (emerged before or after 13 July) or status on their original nests (dominant, non-forager, forager or lone female), or on characteristics of their original nests (bridge girder, number of residents, number of brood, oldest brood stage and number of cells). There were no significant effects (all $p > 0.1$) except for status (change in deviance = 10.4 on 3 d.f., $p < 0.025$). This effect of status was mostly due to dominants being less likely to visit vacated nests (table 2): recoding status to separate only dominants from all other wasps (Crawley 1993, p. 190) produced a non-significant increase in deviance (1.37 on 2 d.f., $p > 0.10$) compared with the model using all four status classes.

We also tested whether characteristics of the vacated nests themselves predicted whether residents would visit them. Vacated nests containing older brood were more likely to be visited (change in deviance = 9.0 on 2 d.f., $p < 0.025$). Recoding showed that this was mainly because nests with pupae were more likely to attract residents than nests in which the oldest brood were eggs or larvae (table 3). Nests on girders 1 and 2, where conditions may have been better (table 1), were also more attractive (table 3: change in deviance = 9.5 on 1 d.f., $p < 0.005$). The total number of brood and number of cells in vacated nests had no effect. There were no significant effects in a similar analysis of visits by floaters (table 3).

The 59 floaters from nests colonized by ants were significantly more likely to visit vacant nests than were residents from unmanipulated nests (table 2: $G = 20.39$, d.f. = 1, $p < 0.001$), suggesting that floaters put more effort into searching. Nevertheless, residents that visited vacant nests usually arrived first, before we had removed any floaters (67% of cases on 25 July, before any floaters had been removed from the population).

(b) *1996: gazebo site*

There were 253 marked nest residents in the gazebo aggregation, but only two moved permanently onto the

Table 4. *Percentage of nests added to the gazebo aggregation that were permanently adopted, in relation to the number of cells, number of brood and oldest brood stage that they contained*

(Bracketed figures give the number of nests in each category. Median number of brood = 9.5; median number of cells = 45.5.)

	no. of brood		oldest brood		
nest size (no. cells)	less than median	greater than median	eggs–tiny larvae	large larvae	pupae
greater than median	25 (4)	100 (6)	25 (4)	100 (2)	100 (4)
less than median	67 (6)	50 (4)	33 (3)	50 (4)	100 (3)

vacant nests that we added to the aggregation. Both movers had previously been non-dominants in groups containing 3–5 residents. A further 11 of the added nests were permanently adopted by floaters, three of which had left their natal nests soon after emerging between 4 and 20 August. The last adoptions occurred on 7 September, and 7 (35%) of the 20 added nests were never adopted despite the presence of numerous floaters.

Nests were more likely to be adopted if they contained more cells, more brood and older brood, and there were significant interactions between these three variables (table 4: oldest brood × cells: change in deviance = 9.58 on 2 d.f., $p < 0.01$; brood number × cells: change in deviance = 6.31 on 1 d.f., $p < 0.025$). Adopting females did not destroy older brood in the nests they adopted. Of the brood originally present in the 13 adopted nests, significantly more of the pupae ($98 \pm 2\%$) and large larvae ($89 \pm 6\%$) than eggs—tiny larvae (at most $33 \pm 7\%$: egg replacement would not have been detected) were still present at the end of the experiment (change in deviance = 39.0 on 2 d.f., $p < 0.001$).

4. DISCUSSION

The ecological constraints model as formulated for cooperatively breeding vertebrates predicts that helpers should leave their natal territories and rapidly fill experimentally created vacancies, as observed in three avian systems (Pruett-Jones & Lewis 1990; Komdeur 1992; Walters *et al.* 1992). In *L. flavolineata*, the obvious analogue of a vertebrate territory is the nest itself. Indeed, Krebs & Davies (1993, p. 345) suggest that '. . . a nest is a scarcer resource for an insect than is a territory for a vertebrate'. However, a main result of our experiments was that non-dominants did not leave existing social groups when we gave them opportunities to nest independently without having to incur nest-building costs (see also Bull & Schwarz 1996; Herbers 1986). Only 5% of the temporary vacancies created in 1995 were permanently filled from a pool of over 200 non-dominants, even though we prevented competition from nest-less floaters. In 1996, 35% of added nests remained vacant despite the presence of 173 non-dominants. These results occurred in a species with nests that are probably unusually costly to construct, and in which residents can potentially take advantage of opportunities elsewhere. Residents do visit foreign nests (table 2), which are easy to locate because of nest-clustering. In total, two-thirds of the residents that visited vacated nests reached them before any floaters, suggesting that searching for vacancies is a viable strategy for residents even when floaters are present. Another experiment we have done indicates that non-dominants are perfectly capable of becoming egg-layers (J. Field & W. A. Foster, unpublished data).

The ecological constraints model also predicts that offspring already in advantageous situations should be least likely to accept opportunities for independent nesting (for vertebrates, see Emlen 1997). In agreement with this, residents appeared to be choosier than nest-less floaters about which nests they visited (table 3), and in 1996 most of the adopting females were floaters. In other respects, however, our 1995 data failed to support the prediction. Residents that visited vacated nests did not tend to come from nests with younger brood or particular numbers of residents or brood per resident. Foragers were no more likely to visit than non-foragers, which rank above them in the queue to inherit the dominant position (Samuel 1987; J. Field and co-workers, unpublished data).

There are two obvious benefits that *L. flavolineata* helpers would forfeit by leaving to adopt vacant nests. First, they may obtain indirect fitness by helping to build and defend their natal nests, and by foraging to feed the brood (Samuel 1987; J. Field and co-workers, personal observations). Second, they can inherit the dominant position on their natal nests. There is a strict age-based queue for dominance (Samuel 1987; J. Field and co-workers, personal observations), but the probability of eventually inheriting is unusually high compared with other social insects: groups are unusually small, and because there is no winter cut-off, waiting to inherit is a viable strategy whenever a female emerges. Incest avoidance is not an issue, in contrast to many vertebrate systems (Emlen 1996). However, if the chance of inheriting drives decision-making, we might have expected low-ranking foragers in the longest queues to be most likely to adopt nests.

A significant feature of our results is the large proportion of vacated nests that were never adopted, particularly in 1996 when no floaters were removed. Our results imply that even floaters prefer to wait for better opportunities rather than adopt nests containing only younger brood. This suggests some additional critical constraint on independent nesting, beyond the costs of nest-building. We speculate that the most likely candidate is a general feature of social insect, but not vertebrate life histories: the long period of offspring dependency in relation to the short life expectancy of adult carers (Queller 1989, 1996; Gadagkar 1990; Reeve 1991). A wasp adopting a nest containing only eggs will obtain zero reproductive success unless she survives almost the entire offspring development period, yet she must undertake risky foraging to feed the brood. Also, her nest must at times be left unattended and vulnerable to usurpation. In contrast, an early death does not necessarily mean total failure for a helper. For example, she will still have part-reared related offspring that other group-members may then bring to adulthood (Strassmann & Queller 1989; Gadagkar 1990).

In *L. flavolineata*, the progressively fed brood takes around 100 days to mature (Samuel 1987), although pupae and large larvae might survive their mother's death if the nest is subsequently adopted (see next paragraph). Assuming exponential survivorship, our field monitoring suggests that lone females are resident for an average of only 44 days (95% confidence interval 30–65, median = 30, $n = 78$ females monitored while alone), and only 10% would be expected to survive 100 days. Samuel's (1987) monitoring of 19 newly initiated nests implies higher survivorship: 37–47% of lone mothers survived until offspring emergence. Both sets of data, however, suggest that a large proportion of lone females fails to produce adult offspring.

The high risks involved in nesting alone would explain why wasps are more likely to visit or adopt nests containing older brood (tables 3 and 4; see also Nonacs & Reeve 1993), and why adopting females choose to rear older brood even though it is unrelated (as in *Polistes*: see Reeve 1991). The older the brood, the less time an adopting female has to wait for the emergence of adults that can continue tending her own brood if she dies. The presence of pupae (table 3) may be particularly important because they are closest to maturity, but do not require feeding with its associated foraging risks (Nonacs & Reeve 1993; Queller 1996). We have observed adopted offspring become helpers when they mature, even when the dominant is unrelated (see also Samuel 1987; Klahn 1988). Younger brood are the most costly to rear, and were much more likely to disappear from adopted nests. They were probably destroyed by adopting females (see, for example, Klahn 1988).

L. flavolineata females usually initiate new nests alone (Samuel 1987). If adopting a nest containing young brood is risky for a floater, initiating a completely new nest must be an option of last resort. Yet nests must sometimes be initiated or there would be no nests. The pay-off to floaters from waiting for better opportunities will depend on parameters such as (i) a floater's age and the survivorship of floaters compared with independent nesters; (ii) the quality of pre-existing active nests and the rate at which they become vacant; (iii) the ratio of floaters to active nests; and (iv) whether floaters have advantages over nest residents in competing for vacancies. Most of these parameters will vary in time and space. Data in Samuel (1987, p. 290) suggest that although *L. flavolineata* nests are initiated throughout the year, initiation occurs particularly at drier times when female density may also be highest.

Ecological constraints are clearly of major importance for the evolution and maintenance of helping in both vertebrates and insects. Our results, however, imply that the constraints involved may be fundamentally different in the two taxa: a territory may be a more valuable resource for a vertebrate than is a nest for a wasp.

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