

High reproductive skew in tropical hover wasps

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A plethora of recent models examines how genetic and environmental factors might influence partitioning of reproduction ('skew') in animal societies, but empirical data are sparse. We used three microsatellite loci to estimate skew on 13 nests of the Malaysian hover wasp, *Liostenogaster flavolineata*. Groups are small in *L. flavolineata* (1–10 females) and all females are capable of mating and laying eggs. Despite considerable variation between nests in parameters expected to influence skew, skew was uniformly high. On 11 of the 13 nests, all female eggs had been laid by a single dominant female. A second female had laid one to two out of 5–10 eggs respectively on the two remaining nests. A likelihood analysis suggested that on average, 90% of the male eggs had also been laid by the dominant. The slightly lower skew among male eggs might reflect the lower average relatedness of subordinates to male versus female offspring of the dominant. We suggest that high skew in *L. flavolineata* may result from strong ecological constraints and a relatively high probability that a subordinate will eventually inherit the dominant, egg-laying position.

Keywords: Stenogastrinae; relatedness; microsatellites; skew

1. INTRODUCTION

Conflicts over reproduction arise in societies of genetically different individuals where more than one individual is capable of reproduction. How conflicts are resolved depends on the payoffs of the different reproductive strategies to each player. Models of reproductive skew examine how stable strategies could evolve to produce the observed variation in reproductive partitioning in animal societies. How any single parameter influences skew depends on assumptions made by the model. By displaying different assumptions and predictions skew models vary in their applicability to different social systems. There is now a need for more empirical tests of the models to analyse conflict over reproduction at the species level (Magrath & Heinsohn 2000).

Skew models can be classified into concession and compromise paradigms (reviewed in Johnstone 2000; Reeve & Keller 2001). We consider models relevant to social hymenopteran societies. Under concession models dominant breeders, who have complete control of subordinate reproduction and group membership, may offer reproductive concessions to subordinate group members in return for cooperation. The reproductive concession offered to a subordinate may depend on the reproductive opportunities elsewhere (Vehrencamp 1983*a,b*; Reeve 1998; Reeve & Ratnieks 1993) or in the future (Kokko & Johnstone 1999; Ragsdale 1999; Reeve *et al.* 2000). (See table 1 for a summary of model predictions.)

Compromise models differ from concession models in that neither dominant nor subordinate has complete con-

trol over reproductive shares or group membership. All group members compete to reproduce, but at a cost to productivity determined by the degree of conflict (Reeve *et al.* 1998). Table 1 summarizes the main predictions made by these concession and compromise models. Despite increasingly elaborate theory, skew and factors influencing it have been quantified in only two hymenopteran species and comparisons with the predictions of transactional models have produced mixed results (Field *et al.* 1998*b*; Reeve *et al.* 2000; reviewed in Reeve & Keller 2001). In this article we quantify variation in reproductive skew and examine potential causal factors in colonies of the hover wasp, *Liostenogaster flavolineata* Cameron (Hymenoptera: Stenogastrinae).

Hover wasps are found in South-East Asian–Papuan rainforests (reviewed in Samuel 1987; Turillazzi 1991, 1996). Nests of *L. flavolineata* are small (up to 90 cells) and are found isolated or in aggregations of sometimes 100 nests or more. Groups usually consist of two to five females, one of which is behaviourally dominant (Samuel 1987). A nest is founded by a single female who rears her brood progressively on insect prey. Newly emerged females may choose to become helpers on their natal nests, where they have the potential to become reproductives, or they may leave and found a nest alone or take over an existing nest. They rarely become helpers on other nests (Samuel 1987; Field *et al.* 1998*a*, 1999). An age-based dominance hierarchy determines the sequence of successive behavioural dominants (Samuel 1987; Field *et al.* 1999). Helping in *L. flavolineata* is truly facultative since all females are physiologically capable of mating and laying eggs (Field & Foster 1999). Conflicts over the production of male and female brood therefore include all colony members. In several respects, particularly the facultative nature of helping, small group sizes and age-based queuing, *L. flavolineata* resembles cooperatively breeding vertebrates (Strassmann *et al.* 1994; Field *et al.* 1998*a*;

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Table 1. Predictions made by concession and compromise models.

(Observed associations in 13 *L. flavolineata* nests are shown. +, – and ‘none’ indicate respectively a positive, negative or no association between the variable and skew.)

relationship with skew	concession models		compromise models		observed in this study
	no future breeding ^a	with future breeding ^b	subordinate inefficiency ^c	restricted access ^c	
genetic relatedness of group members	+	none	none	–	none
fighting ability of subordinates/dominants	–	none	–	none	none
group productivity	+	none	none	none	none

^a Vehrencamp (1983*a,b*) and Reeve & Ratnieks (1993).

^b Kokko & Johnstone (1999) and Ragsdale (1999).

^c Reeve *et al.* (1998).

Shreeves & Field 2002). (Further details of *L. flavolineata*'s biology can be found in Samuel 1987; Strassmann *et al.* 1994; Field *et al.* 1998*a*, 1999, 2000; Field & Foster 1999; Shreeves & Field 2002).

Reproductive skew models are most relevant to the production of sexual brood and not worker brood in eusocial insects. This is because the reproductive value of a sterile worker is negligible relative to a sexual. Since *L. flavolineata* females are behaviourally flexible, distinction between workers and reproductives is unnecessary. In this article we present data on colony-level genetic structure and a maternity assignment analysis to analyse patterns of reproduction in *L. flavolineata*. We discuss our results in terms of reproductive skew models.

2. MATERIAL AND METHODS

(a) Sample collection

The study site comprised an aggregation of 126 *L. flavolineata* nests situated under a bridge on the Old Gombak Road, 30–40 km north of Kuala Lumpur, Malaysia. All wasps resident on the nests were individually marked with enamel paint during 5–13 July 1995 and subsequently monitored for five weeks. Details on site and methods are given in Field *et al.* (1998*a*, 1999). On 8 August 1995, 27 nests with brood and residents were collected. On average, collected nests had 41.39 ± 0.69 (s.e.) cells, contained 24.7 ± 1.81 brood, with 4.92 ± 0.54 potential reproductives (adult females).

(b) Sperm and ovary development

For all 80 adult females, we recorded the number of mature eggs present in the ovaries (eggs more than 1.25 mm long; Field & Foster 1999), the length of largest egg and whether the spermatheca contained sperm. Inseminated spermathecae were removed for DNA extraction in order to obtain the genotype of the sperm.

(c) Molecular techniques

Brood ($n = 243$) from 13 nests were categorized as eggs, small larvae (less than 60 mg), large larvae (greater than 60 mg) or pupae (brood sealed into a pupal cell). Unmarked females that appeared during the two weeks prior to collection were assumed to be newly emerged.

We attempted to amplify individuals at three microsatellite

loci (LF3, LF18 and LF25) using the polymerase chain reaction (PCR) (see Sumner & Field (2001) for conditions, primers and GenBank accession numbers). Products were separated on 6% polyacrylamide gels using standard molecular protocols (e.g. Strassmann *et al.* 1996). Population allele frequencies were calculated using data from the 13 focal nests plus all adults on a further 14 nests. Each locus had between 17 and 33 alleles represented in our samples, with observed heterozygosities of 0.85–0.92. Alleles were scored twice independently by two of the authors.

(d) Genetic structure analysis

All adult females were typed at two to three loci twice to minimize the chance of errors. Brood were typed once at two to three loci. Broods that were homozygous at two to three loci were assumed to be male. The probability of a female being homozygous at all three loci was 1.44×10^{-3} and between 9.6×10^{-3} and 1.2×10^{-2} at two loci. There is no evidence that *L. flavolineata* females mate with more than one haploid male (S. Sumner, M. Casiraghi and J. Field, unpublished data). Relatedness of potential reproductives in each nest was estimated from genotypic data using the program RELATEDNESS 5.0.7 (Goodnight 2000). Colonies were weighted equally and standard errors were obtained by jackknifing over nests.

(e) Brood assignment

The maternity of female and male offspring was analysed using different methods. Females are diploid and can be safely assigned individually to mothers (e.g. Peters *et al.* 1995; Field *et al.* 1998*b*). As males are haploid, the power of individual assignment is unacceptably low. Instead of assigning individual males, we therefore used likelihood analysis to calculate the most probable proportion of male eggs produced by the dominant. The methods are explained in the following text.

(i) Female brood

Two methods were employed to examine skew in female brood. Firstly, in six nests where sperm data were available, broods were assigned as offspring of an adult female when the progeny's genotype contained one of the mother's two alleles and the sperm allele from her spermatheca. The probability that an egg genotyped at the three loci is misassigned to an aunt rather than her rightful mother is less than 1/1800 (following methods of Peters *et al.* (1995)).

The second method of estimating skew, sibgroup analysis, was applied to all 13 nests. Broods were grouped into sibgroups using the program KINSHIP 1.5b4 to calculate sister-cousin log-likelihood ratios for each pair of brood, based on population allele frequencies (Goodnight & Queller (1997); see also Field *et al.* (1998b) for an explanation of methods). Full-sister sibgroups contained no more than three alleles at each locus, with a common allele (the paternal allele) shared at each locus. Any female that fitted into more than one sibgroup was assigned to the largest group. Using our three loci and with the type I error rate set at $\alpha = 0.05$, 8.9% of real sisters were likely to be misassigned as cousins (type II error = 0.089, power = 91.9%). Power was between 70 and 80% for two loci. Broods of similar age were unlikely to be related as aunt-niece because the brood-development period is long (104 days: Samuel (1987)), although the oldest brood could occasionally be aunts of the very youngest brood.

KINSHIP analysis verified maternity assignment and enabled unassigned brood to be placed into sibgroups. Mothers were assigned to sibgroups using genotypes of potential reproductives, ovarian and insemination status and behavioural dominance. Behavioural dominance was based on the percentage time each female spent on the nest (Field *et al.* 1998a; Field & Foster 1999).

(ii) Male brood

Male broods from 10 nests were genotyped. The probability that the observed array of male genotypes was produced by the dominant rather than a subordinate was calculated using maximum-likelihood analysis. The dominant was identified as the female who had laid the female eggs. Where potential reproductives were missing (two nests), subordinate genotypes were pooled to account for the genotypes of uncollected potential mothers (following the methods of Arevalo *et al.* (1998)). On the remaining eight nests, we had collected all potential reproductives and did not pool genotypes: the probability that a given male was the offspring of a subordinate was calculated as the average of the probabilities for each subordinate. The analysis was repeated to determine the most probable proportion of male eggs laid by the dominant as opposed to any other females on that nest who had developed ovaries.

(f) Measuring skew and its correlates

There has been much debate over the choice of skew index in social behaviour and evolutionary studies (e.g. Keller & Krieger 1996; Kokko *et al.* 1999; Nonacs 2000). Choice of index for our study has little influence on the main conclusions because skew is almost always 1.0. We use the program SKEW 1.1 (Krieger & Keller 1997) to calculate a skew index for each nest that takes into account the number of brood analysed. Since the power of assigning male brood individually was low, a skew index was calculated only for female brood. We test whether estimated skew differs significantly from random, i.e. where random represents zero skew with sampling error.

Four potential explanatory variables were quantified to examine their influence on skew: relatedness, relative body size, group size and per capita productivity. Methods of estimating relatedness were explained earlier. Wing cell lengths were used as indicators of body size and relative fighting ability. Two size ratios were examined ((dominant - average subordinate size)/(mean for all females on nest) and (dominant - rank 2)/(mean for pair)). The rank 2 female was taken to be the female who was on her nest 1 most, after the dominant (Field *et al.* 1998a).

Measurements were taken through a binocular microscope using the computer package NIH-IMAGE (1993). Wing-length measurements were repeated for 50 individuals and the resampling error was 0.01%. Group size was taken as the total number of adult females present during the monitoring period (excluding newly emerged females). Per capita productivity was calculated as the total number of brood present at collection divided by group size.

(g) Statistics

Possible associations between skew and potential correlates were explored using general linearized modelling in GLIM (Crawley 1993). The skew index (S) was arcsin-transformed before analysis assuming normal errors. We repeated the analysis using a binary y -variable that took the value 1.0 when skew was 1.0, and 0 when skew was less than 1.0, assuming binomial errors. All four potential correlates were initially included in the model, then terms subtracted until further removals led to significant ($p < 0.05$) increases in deviance, as assessed from tabulated values of f (normal errors) or χ^2 (binomial errors). Data points were nests in both analyses. Estimates are quoted as means \pm s.e.

3. RESULTS

(a) Genetic structure

The average relatedness of female nest-mates for the 13 nests was 0.56 ± 0.054 and 0.52 ± 0.053 for all 27 nests. Both differed significantly from full-sister relatedness of 0.75 ($t_{(0.05(1)12)} = 3.52$, $t_{(0.05(1)26)} = 4.34$, $p < 0.05$). Relatedness estimates are given in table 2. At the colony level, relatedness was found to vary (CV = 34.8): some colonies probably consisted entirely of sisters ($r = 0.75$, $p > 0.05$, $n = 3/27$) whilst for others relatedness did not differ significantly from 0 ($p < 0.05$, $n = 6/27$). Sample sizes of brood available for reproductive partitioning were limited by the small brood size found in *L. flavolineata* nests (mean 24.7 ± 1.81 brood). Of the 88% of the brood ($n = 213$) that were typed successfully at two or more loci, 62% ($n = 131$) were female. Relatedness of nest-mate eggs did not differ significantly from sister ($t_{(0.05(1)12)} = 0.77$), brother ($t_{(0.05(1)9)} = 0.43$) or sibling ($r(\text{female} - \text{male eggs}) = 0.28 \pm 0.042$, $t_{(0.05(1)9)} = 0.71$) relatednesses.

Furthermore, the behaviourally dominant female was more closely related to the female and male eggs than her subordinate nest-mates were (data in table 2; $p = 0.038$, 0.0011, respectively). This suggested that the dominant female laid all the eggs. We explore these data at the colony level through maternity assignment analyses.

(b) Maternity assignment

(i) Female eggs

Sibgroup membership for female brood is illustrated in figure 1. Each column represents a single sibgroup. The number of brood in each sibgroup is displayed above each column, e.g. in nest 30, sibgroup 1 comprised seven eggs and one small larva. We assigned on average $85\% \pm 4.39$ of all eggs in each nest. Reproductive skew amongst female eggs of *L. flavolineata* was high (mean $S = 0.95 \pm 0.033$ (s.e.), range 0.68–1; $n = 13$ nests) indicating that there was normally only one egg layer at any one time, as suggested by the genetic structure analysis earlier.

In 11 out of 13 nests all female eggs belonged to a single

Table 2. Relatedness between brood and adults in 13 nests. (Estimates are $r \pm$ s.e. (number of nests).)

	dominants	subordinates	same sex eggs
female eggs	0.53 ± 0.053 (10)	0.39 ± 0.075 (10)	0.72 ± 0.039 (13)
male eggs	0.47 ± 0.033 (9)	0.22 ± 0.062 (9)	0.52 ± 0.047 (10)

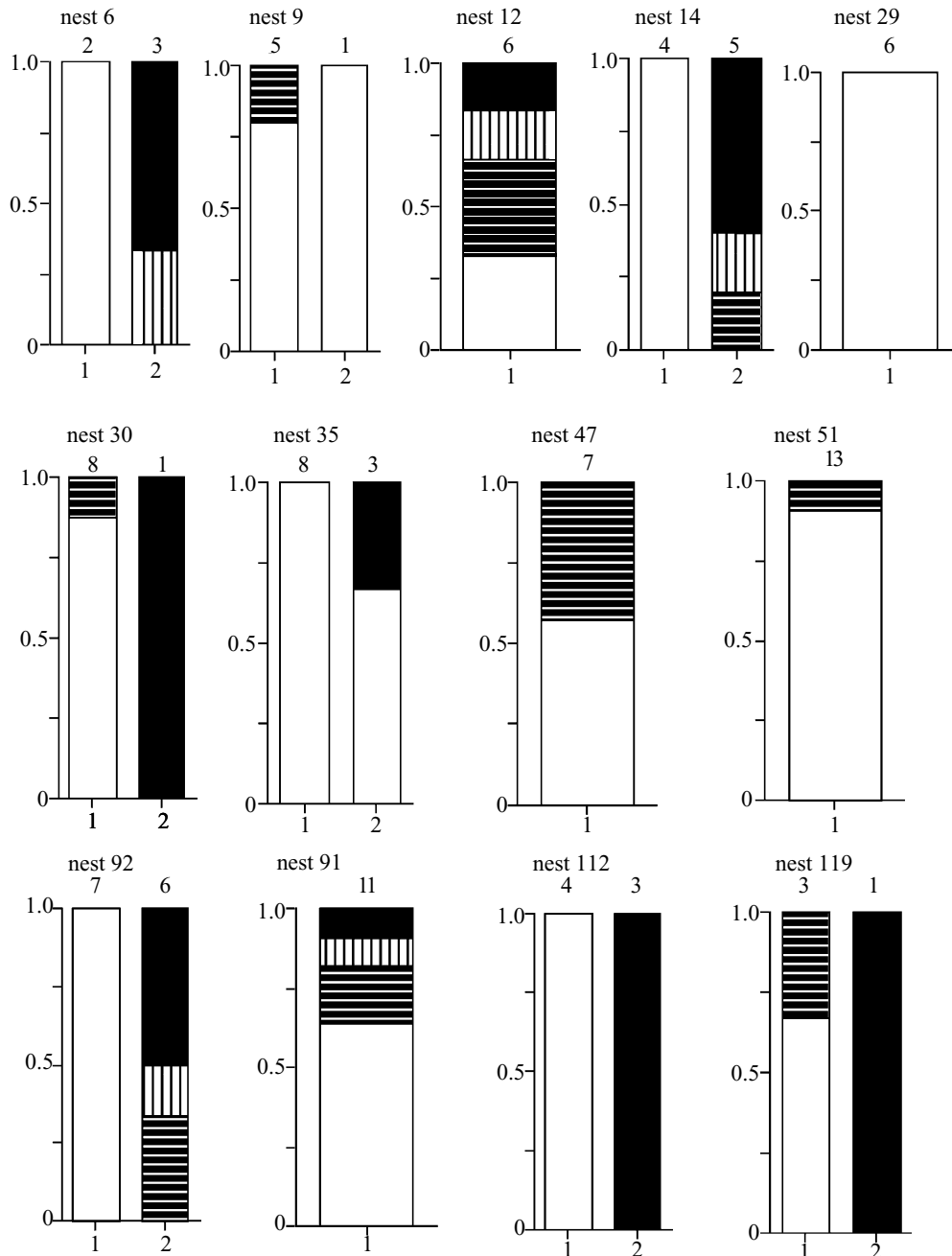


Figure 1. Sibgroup membership for brood in 13 nests of *L. flavolineata*. Columns represent single sibgroups (x -axis). Composition of the sibgroups is indicated by the proportion (y -axis) of different classes of brood. The different shadings represent eggs (white), small (vertical stripes) and large (horizontal stripes) larvae and pupae (black). Numbers of brood assigned are indicated above each column.

sibgroup, indicating a complete skew of 1.0 (see figure 1). In all but one of these nests (nest 6) complete skew was unlikely to have occurred through chance, e.g. as a result of sampling error (see table 3). The mother was identified in nine nests, where she was the only female with a geno-

type compatible with the eggs' sibgroup. In four nests (14, 30, 51, 92) sperm was successfully genotyped and compatible with the eggs' sibgroups. In five nests (12, 29, 47, 92, 119) sperm could not be amplified but in each case only one mated female with developed ovaries had a geno-

Table 3. Skew (S , calculated from Krieger & Keller (1997)) and whether it differs from random.

(Potential skew correlates: productivity, group size (number of potential reproductives, excluding newly emerged females), genetic relatedness r , size ratio A ((dominant – average for subordinates)/(mean for all potential reproductives on nest)) and B ((dominant – rank 2)/(mean for pair)). Means, standard errors (s.e.) and coefficients of variation (CV) are given for each category. Colonies are ranked according to their relatedness estimate.)

nest	S (significant difference from random skew)	group size	size ratios		$r \pm$ s.e. (n females)	per capita productivity (no. of female eggs genotyped)
			A	B		
35	0.68 ^a	4	-0.0099	-0.0297	0.296 \pm 0.046 (6)	5.75 (10)
47	1 ^a	10	0.0252	0.0510	0.344 \pm 0.285 (10)	2.4 (6)
6	1 ^b	4	— ^d	— ^d	0.400 \pm 0.110 (3)	4.5 (3)
30	1 ^a	7	0.0009	0.0122	0.403 \pm 0.093 (9)	5.71 (8)
12	1 ^a	6	0.0472	0.0245	0.448 \pm 0.094 (9)	4.17 (4)
119	1 ^a	4	0.0225	0.0101	0.510 \pm 0.159 (7)	5 (4)
14	1 ^a	6	-0.0007	-0.0109	0.544 \pm 0.156 (6)	3.33 (5)
91	1 ^a	3	0.0015	-0.0347	0.584 \pm 0.144 (7)	7 (7)
51	1 ^a	5	-0.0180	-0.0248	0.618 \pm 0.168 (6)	5.2 (13)
9	0.68 ^b	4	— ^d	— ^d	0.687 \pm 0.103 (5)	5.75 (5)
92	1 ^a	5	0.0257	-0.0233	0.728 \pm 0.227 (6)	4.8 (7)
29	1 ^c	3	-0.0063	-0.0015	0.746 \pm 0.204 (3)	4.33 (6)
112	1 ^c	3	— ^d	— ^d	1.000 \pm 0.000 (3)	6 (6)
mean \pm s.e.	0.95 \pm 0.033	4.92 \pm 0.54	0.0088 \pm 0.0064	0.0027 \pm 0.0087	0.56 \pm 0.054	5.16 \pm 1.39
CV	12.52	39.57	229.98	1018.96	34.8	97.13

^a $p < 0.001$.

^b $p > 0.05$.

^c $p < 0.05$.

^d No data available.

type compatible with the eggs. Mothers were behaviourally dominant, being the colony members that spent most time on their nests and had the most developed ovaries. No mother was assigned on nest 6 where the behavioural dominant was not collected, or nest 112 where two females had genotypes compatible with the eggs and were reproductively mature.

Eggs constituted two sibgroups in nests 9 and 35. Skew was 0.68 for both nests, but differed significantly from random only in nest 35. In nest 9 none of the collected females was inseminated or had developed ovaries. In nest 35 the second egg layer was identified as the previous dominant, who disappeared 23 days prior to collection but whose genotype could be reconstructed from the older brood. Eggs cannot be aged and so it was not possible to determine whether egg laying by new and old dominants overlapped. Hence, skew is between 0.68 (if egg laying overlapped) and 1. With a sequence of dominants, each of which is the sole egg layer during her reign, overlap in egg laying is expected in a fraction of nests equal to t_e/t_{dom} , where t_e is the average developmental period of eggs, and t_{dom} is the average reign of a dominant in days. For *L. flavolineata* this is expected for 15% of nests (where $t_e = 18$ days (Samuel 1987), $t_{dom} = 121$ days (Field *et al.* 1999)). In agreement with our observations (figure 1), we expect eggs to belong to two sibships in 1.95 of our 13 nests.

(ii) Female larvae and pupae

Seventy-two per cent of larvae and pupae were female and they comprised one to two sibgroups (figure 1). In all nests similarly aged brood were usually sisters, suggesting that only one female laid eggs at any one time, that domi-

nance periods were long and that skew did not vary over time.

(iii) Male eggs

The maximum likelihood curve for male production, averaged over the 10 nests, is displayed in figure 2 (solid line) and suggests that 10% of male eggs were not laid by the dominant. In nests 12 and 30, respectively, 20% ($n = 3$) and 43% ($n = 3$) of male eggs were incompatible with the dominant's genotype, but compatible with a single high-ranked subordinate who had developed ovaries. In nest 35, no subordinates had developed ovaries, but the unassigned male had a genotype compatible with the reconstructed genotype of the previous dominant. The likelihood analysis was repeated for these three nests, comparing only the females with developed ovaries. The results (dotted line in figure 2) strongly suggest that male production is shared between the dominant female and the highest ranked subordinate. This analysis gives a minimum estimate of subordinate reproduction since some males may have been wrongly assigned to the dominant and for this reason a skew index was not calculated. The most important outcome of this analysis is that the likelihood of the dominant being the mother of all male eggs is 0.

(c) Skew correlates

Table 3 displays the data used in the generalized linear model. None of the possible explanatory variables showed a significant association with skew (S) in female eggs at the $p < 0.05$ level, but because S was 1.0 for 11 out of 13 nests, the analysis had low power. Nevertheless, explanatory variables were all significantly more variable than

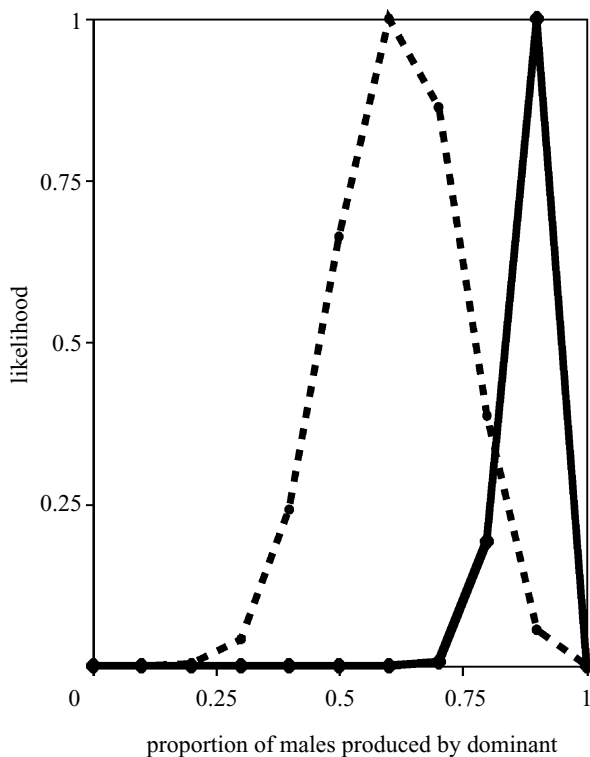


Figure 2. Likelihood curves showing the proportion of males likely to be sons of the dominant, averaged over all nests ($n = 10$; solid line) and averaged for nests with >1 female with developed ovaries ($n = 3$; dotted line).

skew (see table 3 for coefficients of variation; Z -tests_{(0.05(2))}, $p < 0.05$) and this is unlikely to be due to errors in measurements (see § 2). The lack of variation in skew compared with explanatory parameters suggests that reproduction is always monopolized by a single female, irrespective of measured genetic, demographic or morphological factors. Table 1 summarizes our results as a comparison with the skew model predictions. Most notably, these results are contrary to the predictions of all compromise skew models and to those of concessional models that do not consider future breeding benefits.

4. DISCUSSION

We present data on colony-level genetic structure and maternity of brood in colonies of *L. flavolineata*. We show that colony members are closely related and that at any one time, reproduction is usually monopolized by a single female who is the behavioural dominant. The latter finding is consistent with Field & Foster (1999), who studied the same population and found that that in 22 nests only 8% of non-dominant females had developed ovaries. This agrees with ovarian-development data in our 13 nests, where 6 out of 70 (8.5%) non-dominant females had developed ovaries. We also found that high-ranked subordinates, mated with developed ovaries, occasionally laid male eggs but rarely female eggs. Despite considerable variation in genetic relatedness, relative body size, group size and productivity, there was little variation in skew. As shown in table 1, our observations cannot be explained by compromise models, nor by concession models that lack

a future breeding component. However, within the framework of the concessions-based models, the results could be explained through strong ecological constraints on independent nesting (Reeve & Ratnieks 1993; Field *et al.* 1998a, 2000) and a high chance of inheriting dominance (Kokko & Johnstone 1999; Kokko & Lundberg 2001; Shreeves & Field 2002). We examine these in the context of the limited life-history information available for hover wasps and in comparison with studies of reproductive skew in other eusocial insects.

Dynamic models of skew consider how delayed benefits from staying in the group affect skew (Kokko & Johnstone 1999; Ragsdale 1999). If survivorship is high, then the chance of inheriting dominant status in the future, combined with low success of independent nesting, may explain why subordinates remain as helpers without any immediate reproductive incentive (Wiley & Rabenold 1984; Monnin & Ratnieks 1999; Kokko & Johnstone 1999; Shreeves & Field 2002).

Kokko & Lundberg (2001) showed that when survival probabilities between breeding seasons are above zero then the chance of inheriting dominant status in the future, combined with the low success of independent nesting, may outweigh the influence of other factors. Social queues are widely recognized in animal societies and provide a compelling explanation for why subordinates may remain as helpers without any reproductive incentive (Wiley & Rabenold 1984; Monnin & Ratnieks 1999). In *L. flavolineata*, as in many animal societies, dominance is age-based: a subordinate inherits dominance when all her older relatives have died. A subordinate of rank n has a chance of approximately n^{-1} of surviving long enough to reach the head of a queue and become dominant (Field *et al.* 1999). As group size is small in *L. flavolineata* (population-wide averages of three to four females per nest: Field *et al.* (1998a); Shreeves & Field (2002)), queuing is a viable strategy. In addition, the success of breeding independently is low: *L. flavolineata* nests are costly to build and survivorship of lone foundresses is low, with only 10–30% of females expecting to survive the 100 day brood-development period (Field *et al.* 1998a). Shreeves & Field (2002) show that if group sizes remain stable, newly emerged *L. flavolineata* females may expect as much direct reproductive success through queuing as through breeding independently. Furthermore, recent findings in some ant species indicate that queen turnover in eusocial insects may be much more common than previously thought (Heinze & Keller 2000; André *et al.* 2001).

Dynamic skew models predict that high relatedness between breeders and non-breeders is not required for high skew to be stable when future fitness benefits are high (Kokko & Johnstone 1999). Nevertheless, we have shown that nest-mate relatedness is always greater than zero in *L. flavolineata* and so helpers obtain indirect fitness whilst queuing, since productivity increases with group size (Field *et al.* 2000; Shreeves & Field 2002). Furthermore, helpers in *L. flavolineata* have an insurance-based advantage over lone foundresses since, in the event of a helper's death, most of the brood that she partially reared will be brought to maturity by surviving nest-mates (Field *et al.* 2000). Assured indirect fitness benefits and the high

chance of inheriting dominance may together stabilize high skew (Kokko *et al.* 2001).

The breeding regime of tropical species such as *L. flavolineata* is relatively unrestricted by seasonal changes such that the chance of inheritance may be little affected by the time of year a female emerges. Conversely, the chance of a temperate female inheriting reproduction depends on when she emerges during the season. Long-lived organisms with extended colony cycles, such as tropical hover wasps, can afford to wait longer to inherit reproduction than seasonally restricted temperate wasps. Small group sizes, long colony life expectancy and the absence of seasonal constraints on breeding may be reflected in a female's choice of reproductive strategy. This may explain the high, invariable skew in *L. flavolineata* relative to a lower, more variable skew in temperate wasps (e.g. Field *et al.* 1998b; Reeve *et al.* 2000).

Studies on patterns of reproduction in social insects have mostly concentrated on maternity of females (see though Reeve *et al.* 2000). We found that *L. flavolineata* breeders may invest differently in male and female broods, possibly reflecting the asymmetrical relatedness of subordinates to the sons and daughters of their dominant. If subordinates are sometimes daughters of the dominant, as seems probable in *L. flavolineata*, they will on average be more closely related to the dominant's female offspring than her male offspring. We presented genetic data in support of this (see § 3, table 2). This might explain why mated subordinate females tend to produce haploid sons rather than daughters. If skew in male and female progeny often differs in social insects, it may have important repercussions on skew theory and its measurement and should be considered in future studies.

Current opinion is that at the interspecific level patterns of reproduction in small colonies of eusocial insects are controlled by the dominant and generally follow predictions made by concessionary skew models (Reeve & Keller 2001; Sumner & Isaac 2002). Colony-level support is less conclusive: one study provides support for concession models (Reeve *et al.* 2000) whilst two do not (Field *et al.* 1998b; this study). Some aspects of concession models may be more relevant at the species level than the colony level. For example, in social wasps, individuals may be unable to assess their relatedness to the dominant since there is no evidence that they can discriminate within colony relatedness (Queller *et al.* 1990). Kin-selected altruism is more likely to have evolved in response to the average population relatedness rather than on the basis of an individual's ability to distinguish between kin (Keller 1997). More studies on reproductive partitioning among male and female offspring are needed to examine whether concession models explain general patterns of reproduction at the interspecific and colony levels.

The authors thank L. Kirton (FRIM) for assistance in Malaysia, E. Jones and C. Cormack for help with running microsatellite gels, D. Nash for statistical advice, J. J. Boomsma and three referees for helpful comments on the manuscript. This research was supported by a BBSRC studentship to S. Sumner, a N.E.R.C. research grant to J. Field and a Università' di Milano scholarship to M. Casiraghi.

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As this paper exceeds the maximum length normally permitted, the authors have agreed to contribute to production costs.