Rank and colony defense against conspecifics in a facultatively eusocial hover wasp

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An important benefit of social living is increased capacity for defense. Highly eusocial species have often evolved a fighting caste for this purpose, but many facultatively eusocial insects and cooperatively breeding vertebrates lack morphological castes and the decision to defend or not can depend on costs and benefits to each individual. Defense by subordinates in a social group can be regarded as a form of helping, and helping input often varies among subordinates of different age or size. Several hypotheses attempt to explain variation in helping effort, including the effects of relatedness and differences in the costs of helping. Evidence for these hypotheses is mixed and often lacks data on the rank of subordinates, an important determinant of expected future fitness. We examined individual variation in propensity to defend the nest against conspecifics in the tropical hairy-faced hover wasp *Liostenogaster flavolineata*. Prior to experimentation, we determined the positions of all wasps in the age-based queue to inherit the single egg-laying position in each *L. flavolineata* group. Two approaches were then used: observations of defense against natural intrusions by conspecifics and experimental trials where wasps were presented attached to a wire. Higher ranks were more likely to defend the nest than lower ranks, opposite to the pattern previously documented for another form of helping: foraging effort. Possible explanations for this result are that higher ranked females are better defenders and that they suffer a larger decrease in expected future fitness when an intruder usurps their position in the inheritance queue. *Key words:* defense, inheritance, queue, rank, wasp. *[Behav Ecol 18:331–336 (2007)]*

An important benefit of forming social groups is the increased capacity for defense of communal resources. Studies of social defense have focused on how defensive effort depends on the value of the defended resource, such as the developmental stage of offspring or the time remaining before the end of the nesting season (e.g., Judd 2000; London and Jeanne 2003). A second question, however, concerns which individuals in the group choose to defend. In some highly eusocial animals with specialized defensive castes, dominant individuals rarely, if ever, take part in colony defense (Michener 1974; and see references in Judd 2000). In social animals lacking morphological castes, however, individuals have no physiologically predetermined defensive role and have the option to defend or not based on cost/benefit ratios. Data on nest defense in social animals are scarce but provide some interesting contrasts. In naked mole rats (*Heterocephalus glaber*), colony defense against conspecific intruders is undertaken exclusively by subordinates, whereas in the Damaraland mole rat (*Cryptomys damarensis*), defense is undertaken by the dominant (Cooney 2002). In the paper wasp *Polistes fuscatus*, inter- and intraspecific colony defense is principally undertaken by the dominant female (Fishwild and Gamboa 1992; Gamboa et al. 1992; Judd 2000). Defense against conspecifics in the halictine bee, *Lasioglossum zephyrum*, is undertaken by the bee with the second largest ovaries, the "guard" (Bell et al. 1974).

Dominant individuals (queens or breeders) might be expected to defend their investment in offspring and the potential direct fitness benefits of retaining the dominant position. Defense of the colony by subordinates can be viewed as a form of altruism, with an associated personal cost (risk of injury or death) and a range of possible benefits accrued through indirect and direct fitness returns (reviews in Emlen 1997; Heinsohn and Legge 1999). Subordinates can exhibit varied levels of helping effort in social groups (Schmid-Hempel 1990; Reeve 1992; Heinsohn and Legge 1999; Clutton-Brock et al. 2000; Cant and Field 2001), and several mechanisms underlying this variation have been proposed: 1) variation in genetic relatedness between helpers and recipients (Emlen 1991), 2) variation in the short-term costs of helping because of variation in individual condition (Heinsohn and Legge 1999; Clutton-Brock et al. 2000), 3) variation in the expected future fitness benefits that individuals stand to lose through helping (Cant and Field 2001, 2005), and 4) "group augmentation" effects (Kokko et al. 2001). Evidence for the first mechanism, which has most often been examined, is mixed: whereas some studies have found the predicted relationships between relatedness and helping effort, other studies have found no consistent trends (references in Clutton-Brock et al. 2000; Canestrani et al. 2005). In vertebrates, a recent meta-analysis found that only 10% of the variation in helping effort could be explained by variation in genetic relatedness (Griffin and West 2003). Variation in costs to helpers is probably important in some vertebrates and primitively eusocial wasps (Heinsohn and Legge 1999; Clutton-Brock et al. 2000; Cant and Field 2001; Field et al. 2006).

There are limited data available on variation among subordinates in the defensive aspect of helping behavior, particularly in relation to rank. Rank is defined here as an individual's position in the queue to inherit reproductive dominance within its social group, where rank 1 is the dominant, breeding individual, rank 2 is the next in line to inherit the breeding position, etc. Rank is potentially important because it can influence future direct fitness returns through inheritance of the dominant position. Cant and Field (2001, 2005) modeled helping effort based on the trade-off between current investment in help and future reproductive success. They found that, all else being equal, individuals should invest less in helping when expected future fitness is greater. In social groups where queue position is temporally stable,

higher ranked subordinates have greater expected future fitness as they have the greatest probability of inheriting dominance and thus might be expected to work less hard. However, whereas there is evidence that older, higher ranked individuals perform fewer nondefense-related tasks in some vertebrate societies (the naked mole rat; Reeve 1992), the same individuals may show a relatively high propensity to defend the nest against conspecifics (Lacey and Sherman 1991; O'Riain and Jarvis 1997). In this paper, we investigate the relationship between inheritance rank and defense against conspecifics that are potential joiners or usurpers.

The facultatively eusocial hairy-faced hover wasp *Liostenogaster flavolineata* (Hymenoptera: Stenogastrinae) lives in small groups (1–10 females) in relatively aseasonal southeast Asian rainforests. Nests are initiated by a single female and consist of an open mud comb located in moist, protected places such as under rocks or bridges over water. Groups of nests are often spatially clustered. All females are physiologically capable of mating and laying eggs (Field and Foster 1999), but reproduction is monopolized almost entirely by the dominant female (Sumner et al. 2002). Group members inherit dominance according to an age-based queue in which the oldest resident is the egg layer. When the oldest female dies, she is replaced by the next oldest in 90% of cases (Field et al. 2006; Bridge and Field, forthcoming). Colonies can last for several years, with female longevity of the order of 2–3 months for low ranks and 4 or more months for dominant individuals (Field et al. 1999; Shreeves and Field 2002). Relatedness among nest mates is high (approximately 0.5: Sumner et al. 2002; Field et al. 2006). Newly emerged females can remain on their natal nests as helpers or leave to become "floaters" (Field et al. 1999). Floaters may find nests on their own or occasionally join other colonies.

Although predation by ants, other wasps, and birds does occasionally occur (Cronin A, Field J, unpublished observations), *L. flavolineata* has no specialist predators or parasites: nest defense is primarily against conspecifics (Samuel 1987). Nestless floaters are common in nest aggregations, and previous work indicates that they frequently attempt to land on *L. flavolineata* nests and occasionally succeed in usurping or joining groups (Samuel 1987; Field et al. 1998; Bridge C, Field J, unpublished data). Usurpation is an important threat faced by primitively eusocial wasps in general (Reeve 1991; Gamboa et al. 1992).

METHODS

Experimental background

This study used 3 separate nest aggregations of *L. flavolineata* located in culverts beneath a road in a montane region of peninsular Malaysia near Fraser's Hill, approximately 50 km north of Kuala Lumpur. This is the same road used by Field et al. (2000, 2006). Experimental aggregations contained 30–70 colonies each, and an additional 6 sites containing smaller numbers of colonies were used to collect test wasps for presentation trials. Sites used in this study were 200–1500 m apart, and no site switching of wasps was observed during the study. Colonies were monitored during the period 20 March to 17 August 2003. All resident wasps were individually marked and had wing measurements taken at the beginning of this period, then newly emerging females were marked and measured after eclosion (see methods in Field et al. 1999). Because inheritance rank is age based in *L. flavolineata*, the rank and size of all resident wasps were known at the time experiments were undertaken. The average age difference between successive ranks in this population is of the order of 2–5 weeks. For example, the mean ± standard error ages

Table 1

Number of colonies of different sizes (number of females) used in this study from each of the 3 sites

Number of adult females	Site 2	Site 7	Site 8
2	10 (19)	2 (4)	6 (8)
3	8 (13)	1	4 (7)
4	2 (2)	0 (1)	1
5	0	0	1

Figures outside parentheses represent nests used to observe natural intrusions ($n = 35$); figures within parentheses represent nests used for experimental presentations ($n = 54$).

of the rank 1 and rank 2 females on 54 nests were 134 ± 5 and 114 ± 6 days, respectively (wasps already present from the start of observations on 20 March were counted as being born on 20 March). The number of large brood (large larvae or pupae) in each nest was recorded as a measure of "nest value." Investigations of nest defense used a dual approach, involving observations of defense against natural intrusions by conspecifics and the experimental presentation of live wasps on the end of a tether. Experiments and observation of natural intrusions were conducted between June 29 and August 15 using colonies with 2–5 resident wasps (Table 1). No experimental trials or observations were undertaken on days of inclement weather or at nests with only one resident female. Observers were blind with respect to the ranks of resident females in all trials and observations.

Observations of defense against natural intrusions

Observations of natural intrusions were conducted for 1-h periods during the primary foraging period of 7:45–11:00 AM. Small torches were used to observe 1 or 2 closely positioned (within 30 cm) nests, recording all interactions between resident wasps and any intruders (which were usually floaters), as well as how much time each resident wasp spent on the nest. Definitions of behavioral interactions were the same as for presentation experiments (see below).

Presentation of wasps

Because most natural intruders departed after a low-intensity response from nest residents (see Results), we also examined the response to experimentally provided intruders that could be presented for a longer period. We could thus ensure that experimentally presented wasps were unrelated to nest residents and of known size. Conspecific wasps from nonexperimental sites were captured just prior to experiments and kept in the shade in plastic bags until needed. These "test wasps" were attached to the end of a 60-cm-long wire by means of a loop of cotton around the base of the petiole such that wasps could move legs and wings without visible impediment.

A trial consisted of the test wasp being moved slowly toward a randomly selected target nest from a random direction, until either the resident wasps responded or the test wasp made contact with the nest. In the latter instance, the wasp was held in contact with the nest for a maximum of 30 s or until a defensive response was observed. Torches were used to observe resident wasps during trials. Trials were conducted between 1 and 5 PM. Test wasps were used in up to 5 trials each but never on the same nest. Replicate trials at the same nest were excluded from the main analyses and used only in calculation of within-nest correlation coefficients (see below).

Definition of aggression

Defensive responses were scored from 1 to 3 as follows: 1 = approach—the resident wasp rapidly moved toward the foreign wasp without further aggression; 2 = bite/chase—the resident wasp attacked or chased the foreign wasp; 3 = fight—the resident wasp repeatedly bit the foreign wasp or engaged in an extended bout of aggressive contact often culminating in both wasps falling off the nest.

During 40 of 348 experimental presentation trials, all resident wasps fled the nest. Wasps never fled the nest during natural intrusions, and fleeing was likely the result of small handling errors during the presentation of test wasps. Test wasps were not significantly larger in trials where wasps fled compared with those where they defended the nest, and the number of resident females present also did not differ. There were additionally 34 trials where wasps did not respond to presented wasps at all. There was no difference in the number of resident females present or the size of the test wasp when compared with trials that elicited a response. Presentations that led to fleeing or no response were excluded from the analyses below.

Data analysis

Some nests were observed for more than one 1-h period to record natural intrusions. In order to avoid pseudoreplication, however, a single 1-h period was selected at random for each nest for further analysis, giving a total of $n = 35$ nests (Table 1). In addition, we analyzed the defensive responses of only one, randomly chosen individual from each nest. This is because a floater intrusion normally elicited a response from only one nest resident, so that the responses of different individuals on the same nest were not independent.

In the same way, the response of a single nest resident to a single test wasp presentation was randomly selected for each nest tested, with the constraint that no individual test wasp was used more than once in the entire data set. We excluded nests where the test wasp elicited no response or where nest residents fled the nest. This gave a sample size of 54 experimental presentations to different nests (Table 1). Test wasp trial number (whether the wasp presented to each nest was on its first, second, ..., fifth trial) was entered as a potential explanatory variable in all analyses involving experimental presentations. In order to check whether the effect of rank on propensity to defend using the full data set was the same as when a single observation period or experimental presentation was selected for each nest, we calculated the correlation between rank and defensive propensity among all individuals within each nest, combining all observation periods. The resulting correlation coefficients were then subjected to a sign test.

Generalized linear modeling was used to carry out analyses of covariance and multiple regression in the "R" statistical package, version 2.0.0 for Macintosh (Crawley 2005). We assumed binomial or Poisson errors as appropriate. 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 χ^2. We report significance levels for terms when adding them last to this minimal adequate model. When there was significant overdispersion using binomial or Poisson errors, we refitted the model assuming a quasibinomial or quasipoisson error structure, respectively, and assessed significance using F-tests (Crawley 2005). Model assumptions were checked using the plot (model) function in R (Crawley 2005). Effects of rank were the same whether rank was coded as a continuous variable or as a factor in the analyses.
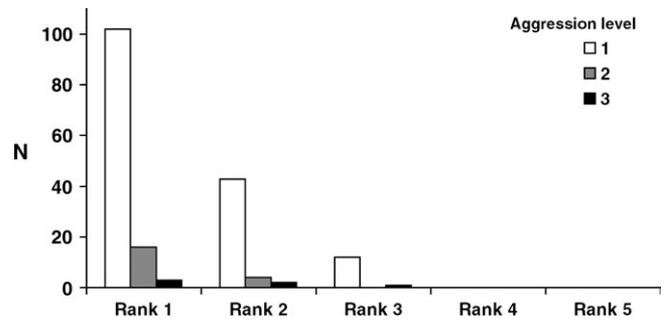
Figure 1
Number of defensive acts of different magnitudes for each rank in response to natural intrusions that occurred during 1-h observation periods at 35 different nests.

RESULTS

Two data sets are analyzed below, the first from natural intrusions and the second from experimental trials where wasps were presented artificially. Instances where only one female was present for any defensive act were not included in analyses of either data set. In the vast majority of cases, only a single wasp defended against each natural or experimental intrusion. The few examples of cooperative defense were excluded from the main analyses and are discussed separately below.
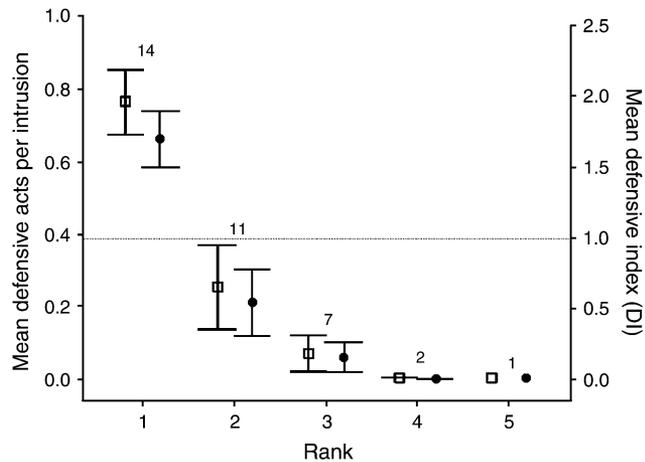
Natural intrusions

There was at least one floater intrusion during 87% of 1-h observation periods. Among nests with at least one intrusion, the number of intrusions was positively correlated with temperature and the number of brood in the nest ($P < 0.0001$ in both cases). In addition, one of the 3 sites had more intrusions per hour than the other two ($P = 0.04$). Time of the day, date, and group size (number of adult wasps present) had no significant effects. Group size is positively correlated with number of brood but had no significant effect on the number of intrusions even when brood number was omitted from the model.

Magnitude of aggression
In most instances when a floater approached a nest, a single female responded rapidly by approaching the floater on landing or just prior to landing, causing the floater to be repelled, usually without contact or a minimum of aggression. The aggression levels observed reflect this: most were level 1 (Figure 1). Because there was no indication that the strength of response was correlated with rank, the number of aggressive responses overall was used to investigate rank effects.

Identities of responding wasps
For each of the 35, 1-h observation periods, a single focal nest resident was selected at random. We analyzed potential factors that could determine the response of these 35 focal wasps to natural intrusions by floaters. The y variable was binomial: the number of defensive responses as a proportion of the number of intrusions that the focal wasp was present for (mean number present for = 4.5). We controlled for group size (Table 1) in the analysis by including number of females as an explanatory factor because the larger the group, the smaller the chance that any individual wasp is the one that defends. The only significant explanatory variable was rank ($P < 0.0001$): higher ranked females were more likely to be the ones that defended the nest (Figure 2). The 14 rank 1 females in the sample defended 71% of intrusions that they experienced; rank 2 females defended 31% ($n = 11$) and ranks 3

Figure 2
Mean (±standard error) number of defensive responses per intrusion (open squares) and mean DI (filled circles) for each rank for natural intrusions. Data are from a single focal wasp from each of the 35 observed nests. Sample sizes are included above each pair of points. The horizontal dotted line indicates a DI of 1.0, which is the value expected by chance if defensive acts were randomly distributed among resident wasps.

defended 4% ($n = 7$). However, the effect of rank appeared to entirely reflect the difference between the dominant and her subordinates: recoding so that all subordinate ranks were combined led to a nonsignificant increase in residual deviance ($P = 0.45$). The focal female's wing length had no significant effect, and there were no significant interactions between rank and site, temperature, time of the day, date or number of brood.

As a further test of rank effects, a defense index (DI) was calculated as the number of interactions performed/number expected by chance (where the latter is the number of interactions for which the focal wasp was present divided by the total number of females present). Spearman correlation coefficients for rank versus DI were calculated for each nest separately, including all individuals and using all replicate data (multiple observation periods for a given nest, if any) in each calculation. The results of these tests were themselves subjected to sign tests. The sign tests indicated a highly significant proportion of negative correlation coefficients ($+ = 6, - = 29$, $P < 0.001$) indicating that high-ranked females had a greater propensity to defend (Figure 2). Although there was a similar trend among only subordinates (when rank 1 females were removed from the analysis), it was not significant ($+ = 4, - = 8, P = 0.39$).
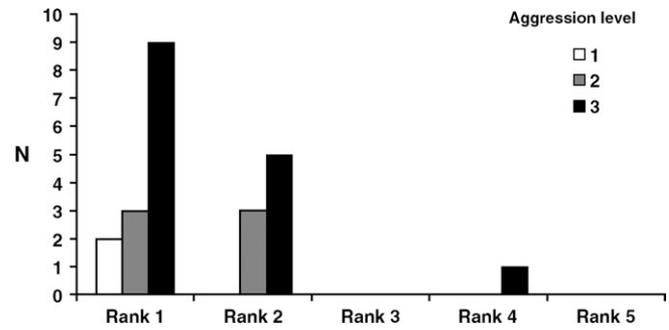
Experimental presentations

Magnitude of aggression
The overall level of aggression in presentation trials was markedly higher than for natural intrusions because presented wasps, unlike natural intruders, could not flee (Figure 3). The level of aggression by the defending wasp did not depend on her rank, group size, or the size of the test wasp presented (Kruskal–Wallis tests, degrees of freedom = 2, $P > 0.1$ in each case).

Identities of responding wasps
For each of the 54 experimental presentations, a single focal nest resident was selected at random. Because only one presentation was made at each nest, the y variable was binary (focal wasp responds or does not respond). Controlling for

group size (Table 1) as before, only rank had a significant effect on whether focal wasps responded ($P = 0.001$): 14 of 21 rank 1 focal females responded, 8 of 21 rank 2s, and 1 of 12 ranks 3–4 (Figure 4). The effect of rank was not a difference between just dominants and subordinates: recoding to combine subordinate ranks led to a significant increase in residual deviance ($P = 0.018$). There was no interaction between rank and other variables tested: test wasp trial number, test wasp wing length, date, time of the day, temperature, or number of brood in the nest.

The correlation coefficient for rank versus DI was calculated for each nest separately using all replicate data and the coefficients subjected to a sign test ($0 = 8, + = 11, - = 34, P < 0.001$), which once again indicated a strong rank effect. There was also a significant effect among subordinates (i.e., when rank 1 females were excluded; $0 = 28, + = 6, - = 19, P < 0.015$).

Joint defense
Joint acts of defense were rare, constituting only 11 acts during natural intrusions and 4 during experimental trials. Of acts observed during natural intrusions, all involved 2 wasps and included the rank 1 individual. In all cases but one, the
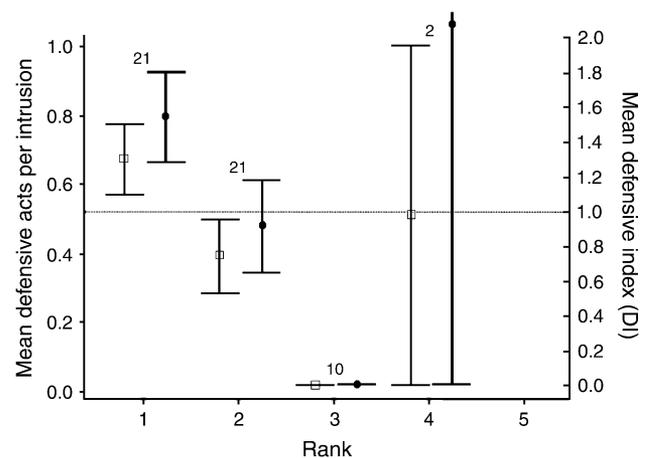

Figure 3
Number of defensive interactions of different magnitudes for each rank, for 54 experimental trials (54 nests). Data are from single randomly selected wasp from each trial nest.

Figure 4
Mean (±standard error) number of defensive responses per intrusion (open squares) and mean DI (filled circles) for each rank for natural intrusions. Data are from a single focal wasp from each of the 54 trials. Sample sizes are included above each pair of points. The horizontal dotted line indicates a DI of 1.0, which is the value expected by chance if defensive acts were randomly distributed among resident wasps.

second wasp was the rank 2 individual. Similarly, during experimental treatments, the rank one wasp was always involved, aided twice by the rank 2 and twice by the rank 3 wasp. Wasp size and magnitude of aggression did not differ significantly from interactions involving only 1 resident wasp.

DISCUSSION

There was a high natural rate of floater intrusion at *L. flavolineata* nests compared with a previous study of *Polistes* (Gamboa et al. 1992). Intrusions were more frequent at nests containing more large brood, and defense normally involved only a single member of the group. Our results demonstrate a strong effect of rank on the propensity to defend against floaters: the dominant defended most often and high-ranked subordinates were more likely to defend than low-ranked subordinates (Figures 2 and 4). This pattern did not occur because high-ranked wasps were more often present on the nest because we analyzed the responses of only the wasps that were present during each intrusion. A similar pattern of defense primarily by the dominant against conspecific intruders occurs in the social wasp *P. fuscatus* and in the Damaraland mole rat (*C. damarensis*) (Gamboa et al. 1992; Judd 2000; Cooney 2002).

Most natural conspecific intruders are repelled with minimal contact in *L. flavolineata* (Figure 1), but defenders may nevertheless risk injury, because interactions occasionally escalate into extended bouts of grappling. Wasps preoccupied with fighting can also fall victim to predators such as spiders (Field J, unpublished observation). Defending can thus be regarded as a form of altruism. The trend for lower ranked subordinates to defend less often is unlikely to be driven by differences in genetic relatedness because relatedness is not correlated with inheritance rank in *L. flavolineata* (Bridge and Field, forthcoming). This suggests that it is ecological costs and/or benefits that covary with rank. It is noteworthy that the trend in defensive behavior is opposite to that observed for another form of helping—foraging effort. In *L. flavolineata*, it is the lowest ranked females that forage the most (Field et al. 2006). This is probably because higher ranked subordinates stand to lose more future direct fitness through costs incurred while foraging because they are near the front of the queue to inherit the egg-laying position (Cant and Field 2001, 2005). The opposite trends for foraging compared with defense could reflect task partitioning, but this begs the question of why it is high-ranked *L. flavolineata* females that defend and low-ranked females that forage, especially because the latter pattern is also found in *Polistes* (Gamboa et al. 1992; Judd 2000; Cant and Field 2001).

The finding that higher ranked subordinates defend more often implies that the pattern of costs and benefits in relation to rank is not the same as the pattern with respect to foraging effort. The age-based inheritance queue means that higher ranked subordinates are on average older than low ranks (Field et al. 2006). Older subordinates might be prepared to bear more costs if they were closer to death, but the evidence available supports the opposite pattern: older, higher ranked females have lower mortality rates, in part, because they forage less (Field et al. 1999, 2006; Shreeves and Field 2002). An alternative explanation for the observed trend is that higher ranking subordinates are better defenders. Being older, they could have more experience of fighting. They could also be of higher intrinsic quality than low-ranked females because they have survived to attain high ranks in the first place. However, body size is not correlated with rank, and all subordinates are capable of reproduction in *L. flavolineata* (Field and Foster 1999; Bridge and Field, forthcoming). High-ranked females could be in better condition than low-ranked females through

preferential access to resources, but this has not yet been investigated.

High-ranked subordinates might defend more if a successful floater intrusion is more costly for them in terms of direct reproduction lost. Floaters may threaten a subordinate's chance of inheritance through usurpation of her rank. If successful joiners take up positions in the queue at random, low-ranked females are most likely to suffer a decrease in their chance of inheritance. However, because the probability of inheritance declines exponentially with rank, demotion by one rank is more costly for high-ranked than low-ranked individuals, so that high-ranked females should invest more in defending their status (Field et al. 1999; Shreeves and Field 2002; Cant and Field 2005; Cant et al. 2006). Regular censuses of nest residents revealed several cases of nest switching. In 12 out of 16 cases, wasps that joined groups of 1–3 females assumed the bottom rank. In 8 of these cases, additional wasps eclosed after the joiner arrived, and assumed ranks below the joiner, but the queue positions of the females present at the time of joining were unaffected. However, in the remaining 4 of 16 cases, joiners usurped the ranks of other females present at the time of joining. In 3 cases, they joined at rank 1, whereas in the fourth case, the joiner assumed the third or fourth rank in what became a group of 5 females. Thus, intrusions may pose a direct threat to status in the hierarchy, and defensive propensity increases accordingly with the value of the rank being challenged. A loss of position in the queue to inherit dominance represents a substantial cost of not defending the nest, potentially countering selection for risk averseness on the part of higher ranked females that are closer to inheriting the dominant position.

In *P. fuscatus*, where data exist for both conspecific and heterospecific invaders, the same individuals are most likely to defend against both kinds of threat (Gamboa et al. 1992; Judd 2000). However, it is possible that inter- and intraspecific threats impose different patterns of costs and benefits in different social groups. More data are needed to understand patterns of individual helping effort in social hierarchies, especially with respect to defensive behavior.

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