Social aggression in an age-dependent dominance hierarchy

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Summary

Social aggression arises from conflicts of interest over reproduction in animal societies. Aggression is often highly variable between individuals in a group, may be correlated with dominance, and is often integral to the establishment of dominance hierarchies that in turn determine reproductive opportunities. However, reproductive dominance is not always linked with social dominance: 'queens' are not always the most aggressive individuals in a group. Furthermore, in some animals social rank is determined without aggression, and derived through another means, such as gerontocracy. In such instances, what is the role of aggression, and what underlies the variation between individuals? Here, we investigate the relationship between inheritance rank and aggression in the hover wasp *Liostenogaster flavolineata*, which has an age-based inheritance queue. All females in this study were of known age and, thus, rank could be determined independently of behaviour. Observations of intra-colony aggression indicated that aggression increased with inheritance rank and occurred among non-breeding subordinates. This cannot be explained by models that do not account for aggression between non-breeders. It is likely that contests over inheritance rank and the higher future fitness anticipated by high-ranking individuals account for this pattern.

Keywords: inheritance queue, social rank, hierarchy, aggression, future fitness.

Introduction

Conflicts of interest arise in animal societies over reproductive inequality and often result in social aggression. In societies of totipotent individuals,

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intra-colony aggression serves a range of possible functions that can broadly be broken up into (i) conflict over work rate and/or worker behaviour (Reeve & Gamboa, 1983, 1987; Reeve, 1992; O'Donnell, 1998, 2001; Sumana & Starks, 2004), (ii) conflict over reproductive apportioning (Reeve & Sherman, 1991; Reeve & Ratnieks, 1993; Clarke & Faulkes, 1997; Faulkes & Abbot, 1997; Reeve & Keller, 2001) and (iii) conflict relating to anticipated future fitness (Cant & Field, 2001; Cant et al., 2006; Field et al., 2006). These conflicts can vary in their influence depending on the environmental, demographic and genetic factors that define the behavioural environment of the individual. For example, conflict over current reproductive apportioning cannot explain aggression between non-reproductive subordinates, but may explain conflict between a reproductive and non-reproductive. A wide range of possible behavioural environments can lead to a high degree of variability in aggressive behaviour between individuals in a group.

Previous studies of behavioural variation in social groups have focussed on helping effort (Heinsohn & Legge, 1999), including foraging (Field et al., 2006), alloparental care (Clutton-Brock et al., 2000, 2001) and colony defence (Cronin & Field, 2007). Efforts to explain within-group behavioural variation through differences in genetic relatedness have met with mixed success (Queller et al., 1990; Keller, 1997; Strassmann et al., 1997; Clutton-Brock et al., 2000, 2001), which has led to investigations of other aspects of the costs/benefits equation that might influence behavioural decisions, such as differences in individual quality, age or experience (Heinsohn & Cockburn, 1994; Boland et al., 1997; Clutton-Brock et al., 1998, 2000; Heinsohn & Legge, 1999) or differences in anticipated future fitness (Cant & Field, 2001; Cant et al., 2006; Field et al., 2006). In vertebrate societies, differences in experience, size or ability may explain behavioural variation (Reeve & Sherman, 1991). In many insects, however, these traits exhibit relatively little variation between individuals and, thus, may not explain the behavioural variation within a group. Recent studies have argued that the missing factor in such instances is inheritance rank (Cant & Field, 2001, 2005; Cant et al., 2006). In many social animals, opportunities for the greatest (or only) fitness gains are derived from inheritance of the dominant, breeding position. In this regard, position in a queue to inherit, or inheritance rank, is a major determinant of anticipated future fitness. Where other factors such as size and individual quality are equal, anticipated future fitness has the potential to be a major factor influencing individual behavioural variation. Field et al.

(2006) demonstrated that individuals nearer the front of an inheritance queue are less likely to indulge in costly or risky foraging, presumably because they have the greatest chance of inheritance and hence more to lose (Cant & Field, 2001, 2005). Fighting for a position in a queue is, thus, a means of contesting future anticipated reproduction. Furthermore, as the probability of inheritance is greatest nearer the front of the inheritance queue, the value of the contested position increases accordingly. Cant et al. (2006) propose a model of this system based on anticipated future fitness, that predicts increasing aggression toward the front of a queue to inherit, and that aggression will be more common in larger, more productive groups. In co-foundress associations of *Polistes*, they found that aggression increased with social rank, but there was no evidence for an effect of group size.

Variation in aggression between individuals is often correlated with social rank in animal societies, with higher ranks exhibiting higher rates of aggression (Cant et al., 2006; Clarke & Faulkes, 2001). However, 'queens' are not always the most behaviourally dominant individuals (Sumana & Gadagkar, 2001), and aggression may vary over time (Premnath et al., 1996), with increased levels of aggression associated with initial establishment of ranks in newly formed groups (e.g., *Ropalidia marginata*; Premnath et al., 1996; Sumana & Gadagkar, 2001) and replacement of dominants (e.g., naked mole rats; Clarke & Faulkes, 1997: Ponerine ants; Monnin & Peeters, 1999). However, if ranks are established through other means, such as a gerontocracy, what then is the role of aggression? If social dominance is not openly contested, what drives aggression and governs the variability between individuals? Here, we examine the role of social aggression within colonies of the hairy-faced hover wasp *Liostenogaster flavolineata*, a species with a single breeding female and an age-based queue to inheritance of the dominant position.

Liostenogaster flavolineata Cameron (Hymenoptera: Stenogastrinae) is a facultatively eusocial hover wasp that inhabits the relatively aseasonal environments of South-East Asia. There is no pronounced annual nesting cycle, with continuous brood-rearing throughout the year. Colonies consist of up to ten females that progressively rear brood with insect prey. Single females initiate nests in moist, protected environments such as under rocks or bridges, where aggregations of sometimes hundreds of nests can develop. Colonies can potentially last indefinitely, since dominants can be replaced from within

the group and nests are physically robust. There is an age-based queue to inherit dominance and the dominant is the oldest female in the group. Female longevity is of the order of 2-3 months for low ranks and 4 or more months for dominant individuals (Field et al., 1999; Shreeves & Field, 2002). The dominant females monopolises reproduction with little or no subordinate reproduction occurring (Sumner et al., 2002). Inheritance of the dominant position, thus, provides the only opportunity to reproduce directly without leaving the colony. Newly emerged females are not physiologically constrained, and may remain to help on the natal nest or disperse to found their own nest. Thus, these societies resemble many cooperatively-breeding vertebrates in that colonies are relatively small, dominance is age-based, and helping is facultative (see also Samuel, 1987; Field et al., 1998, 1999, 2000, 2006 for more information on *L. flavolineata*).

Materials and methods

This study used three aggregations of the hover wasp *L. flavolineata*, located in culverts beneath the road in a montane region of peninsular Malaysia near Fraser's Hill, approximately 50 km north of Kuala Lumpur. Aggregations contained 30-70 colonies each of 1-10 wasps, though this study used colonies of 2-5 females only. All resident wasps were individually marked and had wing measurements taken at the beginning of the study. Colonies were monitored during the period 20 March to 17 August 2003 with evening censuses every 2 days. Brood mapping combined with monitoring of unmarked females allowed us to track the emergence of new females and mark and measure them as they emerged. Observations of intranest interactions were undertaken between June 29 and August 15. No observations were undertaken on days of inclement weather. For further details on basic methodology see Field et al. (1998, 1999, 2000, 2006).

As *L. flavolineata* has an age-based queue for dominance, the rank of all residents could be determined once newly emerged wasps, for which the date of emergence was known, had replaced the wasps that were present initially. This method provided us with a system of ranking individuals that was independent of behaviour. In the few instances in which more than one old wasp remained when observations began, ranks were determined using a repeated daytime census, which is an effective means of identifying the dominant (Field et al., 1998, 1999, 2000).

Observations periods were in 1-h blocks during the primary foraging period between the hours of 07:45 and 11:00. Observers used small torches and monitored one or two adjacent (within 30 cm) nests, recording all interactions between resident wasps, as well as time spent on the nest and foraging related interactions.

Definition of aggression

Although some authors have questioned the role of 'aggressive' acts like darts (Sumana & Starks, 2004), our observations suggest that low level aggressive acts would often escalate into fights if some response was not elicited from the recipient, and all such interactions were treated as forms of aggression here. Interactions were scored from 1 to 3 as follows; 1 = approach/dart — the initiating wasp rapidly approached the receiving wasp; 2 = bite/chase — the initiating wasp attacked (bit) or chased the receiving wasp; 3 = fight — the initiating wasp repeatedly bit the receiving wasp or engaged in an extended bout of aggressive contact, often culminating with both wasps falling off the nest. Where an interaction began as an approach and developed quickly into a chase or bite, this was scored as a single level 2 interaction. Interactions were scored separately only when separated by a period of quiescence.

Data analyses

Statistical analyses were performed using the 'R' statistical package (Crawley, 2005), with all potentially explanatory factors (rank, time present on the nest, nest, date, number of adult females, site, wing length, number of brood, temperature, and time of day) initially included and poisson or gamma errors assumed as appropriate. Poisson models were remodelled with quasipoisson errors when analyses of residual deviance indicated overdispersion. Starting with interaction terms, we 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 with Poisson errors and F with Gamma errors. Significance values are reported for terms added to this minimum adequate model.

Our data set comprised 148 interactions from 25 colonies and 36 observation periods. As some colonies had repeated observations, 'nest' was included as a potential explanatory factor in all analyses. Interactions related

to foraging (defined as within 30 s of a wasp returning to a nest) were excluded from analyses. There were 9 colonies of two females, 17 with three females and 5 colonies each of four and five females. There was a mean of 3.17 ± 0.16 females per colony over the 36 observation periods, and the number of females did not differ between sites ($\chi_6^2 = 10.63$, $N = 36$, NS). Time on the nest was included as a potential explanatory variable in generalized linear models because higher ranks spent more time on the nest than lower ranks (Kruskal-Wallis: $\chi_4^2 = 43.0$, $p < 0.001$) and, thus, had more opportunity to partake in aggressive interactions. In dyadic analyses, variation in aggression between dyads (ranks 1 and 2, ranks 2 and 3, etc.) was considered in total, and divided into 'displays' (higher to lower directed aggression) and 'tests' (lower to higher directed aggression).

Results

Generalized linear modelling indicated that overall aggression level per colony (number of acts per observation period) did not differ between sites, and was not dependent on brood present, number of adult females or any of the environmental variables.

Intensity of aggression

Table 1 summarises the number of interactions of different intensities initiated by each rank. The proportion of acts of different intensities did not differ between ranks (Chi-square test: $\chi_6^2 = 1.02$, $N = 148$, NS), and, thus, acts of all intensities were pooled and considered together. Rank 1 females initiated 78% of interactions overall, with 12% by rank 2, 9% by rank 3 and 1% by rank 4 females.

Table 1. Total number of aggressive acts of different intensity performed by females of each rank.

Aggression level	Rank 1	Rank 2	Rank 3	Rank 4
1	104	16	12	1
2	11	1	2	
3	1			

Frequency of aggression

An analysis including all potential explanatory factors indicated a significant effect of rank ($p < 0.001$) and time on the nest ($p = 0.002$) on number of acts initiated per observation period, but no effect of other factors and no interactions. Aggression rate varied with rank as shown in Figure 1.

Dyadic analysis

The rate of aggression (interactions per minute present) toward adjacent ranks was double that toward all other ranks overall (mean ($\pm$ SE) for adjacent ranks = 0.0036 ± 0.00045 versus 0.0018 ± 0.00053 for other ranks). However, proportion of interactions that were between adjacent ranks was not different to that expected by chance when broken into groups based on the number of females, as nests with fewer females should have a higher proportion of adjacent interactions. The rates of tests and displays for each dyad group are summarised in Figure 2, which shows a trend of higher aggression
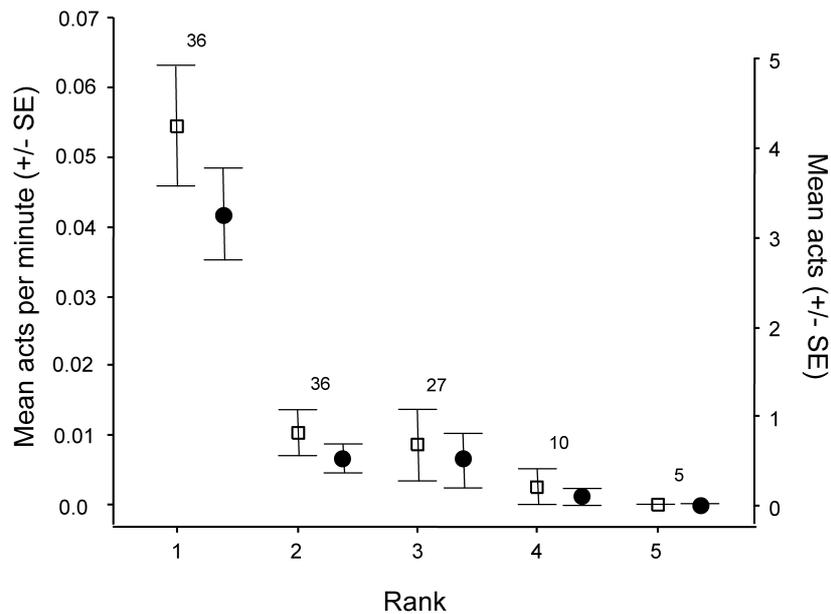

Figure 1. Mean ($\pm$ SE) intracolony aggressive interactions initiated per minute (open squares) and per observation period (closed circles) for each rank. Figures above error bars indicate sample sizes (number of observation periods).
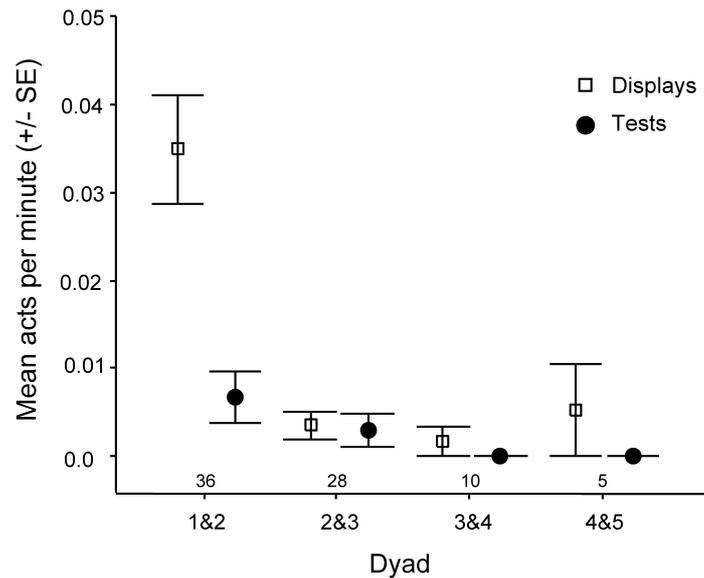
Figure 2. Mean (± SE) interactions initiated per minute on the nest for each dyad (e.g., 1 & 2 = interactions between rank 1 and rank 2), divided into 'tests' (open squares; from low rank toward high rank) and 'displays' (closed circles; high toward low rank). Figures above error bars indicate sample sizes (number of observation periods).

rate among higher ranked dyads. Furthermore, the disparity between 'displays' and 'tests' is most marked in the highest ranked dyad. Generalized linear model analysis indicated that number of acts was dependent on dyadic rank ($p < 0.001$) and time on the nest ($p < 0.001$). Time on the nest only was significant for aggressive 'tests' ($p < 0.001$), whereas dyadic rank only was significant for aggressive 'displays' ($p < 0.001$).

Discussion

Reproduction in *L. flavolineata* is almost entirely monopolised by the dominant female: approximately 8% of subordinates have developed ovaries and though they may occasionally lay male eggs, rarely lay female eggs (Field & Foster, 1999; Sumner et al., 2002). Aggression between dominant and subordinate individuals is, thus, unlikely to result from conflict over current reproductive opportunities. Aggression among non-reproductive subordinates is also unlikely to be explained by conflict over current reproduction

(though aggression among subordinates may act as a means of regulating task performance in some taxa; O'Donnell, 2001). Predictors of aggression such as 'work-conflict' (Reeve, 1992; Jacobs & Jarvis, 1996) and 'ovarian suppression' (Faulkes et al., 1990) attempt to explain competition over current reproduction between breeding and non-breeding females, and are unlikely to explain the observed patterns in *L. flavolineata*. Finally, relatedness is not correlated with rank in *L. flavolineata* (Bridge & Field, in press), and, thus, genetic differences cannot explain the observed trend in aggression. The available data are consistent, however, with aggression in *L. flavolineata* being derived from a contest over social rank itself.

The existence of an inheritance queue in a social group establishes fundamental differences in the anticipated future fitness of group members, with higher ranks having the most to lose and, thus, the most to fight for. Cant et al. (2006) developed a model of this system that predicts increasing aggression toward the front of a queue to inherit the dominant position, when the contested resource is position in the queue rather than an immediate share of reproduction. Fighting, thus, occurs over rank, and this model has the advantage of providing an explanation for aggression between non-reproductive subordinates. Cant et al. (2006) found evidence consistent with the predictions of their model in the paper wasp *Polistes dominulus*. They also demonstrated a strong effect of date on aggression, with aggression increasing with decreasing breeding opportunities toward the end of the season. The rate of aggressive interactions initiated by females of *L. flavolineata* increased with increasing rank, though in an interesting contrast to the Cant et al. (2006) data, there were no seasonal patterns in aggression. The length of our observation period was limited, but no seasonal trends might be expected in *L. flavolineata* because breeding is aseasonal and continuous.

Although dominant females were by far the most aggressive, aggression occurred among all dyads and increased in frequency with increasing rank. The number of aggressive acts was influenced by the amount of time present on the nest, which was significantly biased in favour of higher ranks, but the rank trend remains clear in plots of interactions per minute present (see Figures 1 and 2). Dominant individuals are frequently the most aggressive in social groups (Chandrashekara & Gadagkar, 1991; Monnin & Peeters, 1999; Faulkes & Bennett, 2001), though patterns of aggression among subordinates may be less clear. In the naked mole rat (*Heterocephalus glaber*) and queenless ants (*Dinoponera*), dominant individuals are the most aggressive,

(Hart & Ratnieks, 2004; Monnin & Peeters, 1999), and specific forms of aggression are used for this purpose by dominants only ('shoving' in mole rats; Lacey et al., 1991, and 'blocking' in *Dinoponera*; Monnin & Peeters, 1999). Breeders in *L. flavolineata* did not exhibit behaviourally unique forms of aggression relative to subordinates, which could stem from a need for all ranks to constantly reinforce their position in the hierarchy. As inheritance order is well defined by relative age in *L. flavolineata* (Bridge & Field, in press), constant maintenance of this hierarchy may entail signalling in the form of aggression. Ranks below the top subordinates are less clear in *Dinoponera* (Monnin & Peeters, 1999) and naked mole rats (Clarke & Faulkes, 1997), and aggression among subordinates escalates during a scramble for dominance when queens die. In contrast, there is no evidence for an increase in aggressive activity during succession to dominance in *L. flavolineata*. In other taxa, aggression among subordinates can also be explained as a means of regulating task performance (e.g., *Polybia occidentalis*; O'Donnell, 2001), and over a conflict in interest over the identity of the breeder (Hart & Ratnieks, 2004). However, the available data suggest that aggression in *L. flavolineata* is not correlated with helping effort (Cronin, unpub.) or relatedness. Analysis of dyadic interactions in *L. flavolineata* indicates that 'displays', or top-down aggression was more common than 'tests', and occurred when 'tests' were rare or absent. This suggests that top-down aggression might be an effective means of deterring challenges and/or signalling status, and could serve to reinforce the stability of the age-based hierarchy.

Inheritance of the dominant position provides the only opportunity for direct reproduction within a *L. flavolineata* group (Field et al., 2006). Previous studies have demonstrated that higher ranked subordinates forage less, presumably because they have more to lose (Field et al., 2006). In contrast, the propensity to defend the nest against conspecific intruders in *L. flavolineata* increases with rank. The latter trend likely stems from the fact that intruders can usurp ranks and, thus, defence of the nest is effectively defence of an individual's inheritance status (Cronin & Field, 2007). Similarly, the increase in frequency of intra-colony aggression with rank is also likely to be related to the value of the contested resource:inheritance rank. Position in the inheritance queue is age-based rather than ability-based, and there is no correlation between size and rank in *L. flavolineata* (Field et al., 2006; Bridge & Field, in press). Thus, risks associated with fighting are likely to be similar for all ranks on average, whereas the value of the contested rank increases toward

the dominant position. While higher ranked individuals are less likely to participate in risky foraging (Field et al., 2006), these same individuals have the highest frequency of aggressive encounters with nest mates, suggesting that the potential benefits of contesting a rank shift or defending one's position in the hierarchy outweigh the potential costs of fighting. Further studies of aggression, particularly among subordinates, are needed from other taxa to assess the pervasiveness of these trends.

Acknowledgements

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