

Queuing for dominance: gerontocracy and queue-jumping in the hover wasp *Liostenogaster flavolineata*

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Received: 17 April 2006 / Revised: 31 December 2006 / Accepted: 5 January 2007 / Published online: 2 February 2007
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Abstract The mechanisms through which dominance is inherited within social groups vary from direct interactions such as fighting to non-confrontational conventions. *Liostenogaster flavolineata* is a primitively eusocial hover wasp in which one female, the ‘dominant’, is the only reproductive upon the nest. The remaining females, although capable of reproduction, behave as helpers. In this study, we investigate the rules by which helpers inherit dominance. We removed successive dominants from 56 nests and recorded accession on un-manipulated nests. The results showed that *L. flavolineata* has a strict age-based inheritance queue: new dominants are the oldest female in their groups 87% of the time. Thirteen cases of queue-jumping were found in which young individuals were able to supplant older nestmates and inherit dominance precociously. Queue jumpers did not differ from other wasps in terms of relatedness to other group members or body size. Individuals that had previously worked less hard than other females of equivalent rank were significantly more likely to later jump the queue. Queue-jumping may represent a cheating strategy or could indicate that the rule for inheriting dominance is not based purely on relative age. We also discuss possible reasons why age-based queuing has evolved and its potential to promote the evolution of helping behaviour.

Keywords Convention · Inheritance · Dominance · Eusocial · Wasp

Introduction

In primitively eusocial and cooperatively breeding societies, individuals known as ‘helpers’ forego their own reproduction and instead rear the offspring of a queen or breeding pair. However, helpers may themselves eventually inherit a dominant, reproductive position within the group. Models showed that if the likelihood of achieving dominance is large enough for a helper, this may provide a sufficient incentive for staying in the group, even when intra-group relatedness is low (Wiley and Rabenold 1984; Stacey and Koenig 1990; Dunn et al. 1995; Shreeves and Field 2002; Queller et al. 2000; Buston 2004). Achieving direct fitness is more likely for subordinates in small groups where there are fewer competitors (Kokko and Johnstone 1999; Ragsdale 1999; Shreeves and Field 2002).

Apart from group size, an individual’s chance of attaining a dominant position will depend on the rules through which dominance is determined. In vertebrates that compete for access to mates or food, dominance may be determined through fighting, and a hierarchy may emerge, which is based largely upon body size (e.g. Veiberg et al. 2004). Larger individuals are likely to be the strongest and most effective of contenders (Appleby 1983). Alternatively, dominance can be determined through phenotypic traits that advertise their owner’s genetic fitness, such as colour or song (e.g. Parsons and Baptista 1980; Rohwer 1985). Facial colouration influences reproductive dominance in the facultatively eusocial wasp *Polistes dominulus* (Tibbetts and Dale 2004).

Fighting has less often been implicated in determining dominance in eusocial groups. A possible mechanism for determining dominance in such groups is the use of a convention (Strassmann and Meyer 1983; Seppä et al. 2002). We define a convention as a system in which an

Communicated by K. Ross

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individual possesses a unique attribute that merely singles it out as the next dominant without reflecting its quality. Conventions may minimize group-level costs through fighting, but because dominance is not then linked to individual quality, group members may suffer reduced productivity when a poor quality individual becomes dominant. One possible example of a convention is ‘gerontocracy’ in which dominance is based upon seniority within the group, as recorded by Strassmann and Meyer (1983) in the paper wasp *Polistes exclamans*. Age-based queuing for reproductive dominance is thought to occur in many primitively eusocial insects and cooperatively breeding vertebrates (Shreeves and Field 2002). Theoretical models of social behaviour often assume a gerontocracy, but how strictly the age rule is obeyed has rarely been tested.

All else being equal, every individual in a eusocial group should prefer a dominant, reproductive position over being a helper, even if helping is only temporary. The dominant will be more closely related to the offspring reared by the group and in eusocial insects suffers less exposure to predation because she rarely if ever leaves the nest. This raises the possibility that individuals could attempt to cheat by ignoring the rules through which dominance is normally attained (Johnstone and Grafen 1993). If dominance is acquired through ritual or actual fighting, the quality of an individual determines its success. Conventional mechanisms for acquiring dominance may be more vulnerable to cheating because the dominant is not necessarily the individual with the greatest resource-holding potential and may therefore be usurped more easily. Natural selection might be particularly likely to favour cheating by a helper that is unrelated to other group members, so that her only method of gaining fitness is through direct reproduction. Alternatively, in the same situation selection might favour other group members preventing the unrelated individual from attaining dominance. In this paper, we investigate age-based queuing and the possibility of cheating in the primitively eusocial hairy-faced hover wasp *Liostenogaster flavolineata* (Hymenoptera: Stenogastrinae).

L. flavolineata lives in groups of typically 1–5 (up to 10) females on mud nests in the Southeast Asian tropics. Female nestmates are close relatives (mean coefficient of relatedness approximately 0.5), typically sisters or cousins (Sumner et al. 2002; Field et al. 2006). A single female in each group, known as the dominant or rank 1, lays almost all of the eggs and rarely leaves the nest (Field and Foster 1999; Sumner et al. 2002). Helpers (rank 2 downwards) forage to feed the immature offspring, but can become egg-layers given the opportunity (Field and Foster 1999). Small group sizes and the aseasonal tropical environment imply that direct fitness through inheriting the dominant position could be a large component of lifetime fitness for helpers in *L. flavolineata* (Field et al. 1998, 2000). Previous work

suggests that inheritance of the dominant position may be gerontocratic, but detailed data are lacking (Samuel 1987; Field et al. 1999; Shreeves and Field 2002). Whether any gerontocracy is truly conventional is also unknown because age could correlate with other traits that allow individuals to assume dominant positions, such as larger size or greater experience. We explore some of these traits within this system.

Materials and methods

To determine whether dominance is inherited gerontocratically in *L. flavolineata*, we used two methods. First, we experimentally removed successive dominants from nests and determined the relative age of the new dominants. However, because queuing time was thereby reduced, there were more likely to be females of similar age potentially competing for the vacant dominant position: some individuals that would normally have died during the wait to inherit would still be present, reducing the gaps in age between successive individuals. Our second method was therefore to determine the order in which un-manipulated individuals of known age inherit dominance naturally. Because of mortality during the wait to inherit dominance, the gaps in age between the oldest residents will tend to be larger on un-manipulated nests. The study was carried out upon a population of *L. flavolineata* near Fraser’s Hill, Pahang State, Peninsular Malaysia (Field et al. 2000; Shreeves and Field 2002). The study sites were culverts carrying streams under the road between Fraser’s Hill Gap and Raub.

Dominant removals in 2001

Fifty-six nests were chosen, these being all of the nests in 4 culverts that had more than one resident female on August 28, 2001 (18 nests at site 2, 1 at site 3, 13 at site 4 and 24 at site 5). The relative ages of most of the wasps on these nests were known through intensive monitoring during the preceding 5 months, during which each newly emerged female was individually marked soon after she reached adulthood. A female was assumed to be newly emerged if she was unmarked and if her first appearance coincided with the disappearance of the mud cap that closes a pupal cell (for further details see Field et al. 1999). The relative ages of some wasps were unknown, either because they had reached adulthood before monitoring began or because they had joined the group from an unknown source. In addition, more than one newly emerged female sometimes appeared at the same time, so that their ages were tied.

On 28th and 29th of August, the identity of the dominant (rank 1) female on each nest was determined by censusing every 30 min during the main foraging period (0700–1100

hours). For every census, the identities of the females present on each nest were recorded. Dominants do not forage for larval provisions and rarely leave the nest (Field and Foster 1999; Cant and Field 2001; Shreeves and Field 2002). The dominant on the nest was assumed to have been identified if there was one female that had been present on at least three more censuses than any other nest resident. On nests where no dominant could be identified in this way, censusing continued beyond August 29 until the dominant's identity became clear. If necessary, behavioural observations were used to confirm the dominant's identity. Past studies have confirmed that such criteria are effective in establishing dominant identity (Field and Foster 1999; Cant and Field 2001). In practice, identification of most dominants was clear-cut: dominants were present for $97.8 \pm 0.41\%$ censuses compared with $68.7 \pm 2.97\%$ for the female that was present next most often.

Once the dominant on nests with three or more residents had been identified, she was permanently removed (Table 1). The identity of the new dominant was then determined by censusing/behavioural observations in the same way as before; starting 1–2 days after the original dominant had been removed. Once she had been identified, the new dominant was herself removed and the procedure repeated until only two females remained, when no further removals were required to determine inheritance ranks. In this way, we determined the inheritance ranks of as many as possible of the wasps originally present. Spearman's Rho was used to estimate the correlation between relative age and inheritance rank. Females were frozen and the right forewing of each wasp placed between two microscope slides. Wing length was estimated as the length of the first discoidal cell viewed through a binocular microscope using the software NIH Image (<http://rsbweb.nih.gov/nih-image/about.html>). Females that inherited dominance ahead of at least one unequivocally older female were designated as 'queue jumpers'.

Table 1 Successive removal of dominant individuals to determine inheritance rank

Inheritance Rank	Time 		
	1	Dominant 1	Removed
2	Subordinate 2	Dominant 2	Removed
3	Subordinate 3	Subordinate 3	Dominant 3
4	Subordinate 4	Subordinate 4	Subordinate 4

Natural inheritance

In the 2001 dominant removals, only the females that were already dominant at the start of the experiment had acceded to rank 1 naturally. To further compare the results of experimental removals with natural accession, we examined a second dataset collected by A. Cronin and J. Field in 2003 (see Field et al. 2006). This dataset was from nests in culverts under the same road as in 2001. The relative ages of resident females had been determined through monitoring for the 5 months up to the end of August 2003 using the same methods as above. Dominants were then identified using half-hourly censuses between 0700 and 1100 hours on August 20–31. We used these data to determine the proportion of nests on which the dominant was also the oldest female resident. We also checked for evidence of queue-jumping in a third dataset collected in 2002 in which a further 51 nests were monitored over a 6-month period using the same methods as above.

Genetic analysis

To determine how closely related queue jumpers were to their nestmates, females from the 2001 dominant removal study were genotyped at three microsatellite loci previously developed for *L. flavolineata*: loci LF25, K18 and I3 (Sumner and Field 2001). ³²P-labelled PCR products were separated by running them on 6% polyacrylamide gels following the standard methods in Strassmann et al. (1996) and Sumner et al. (2002). Population allele frequencies were calculated using data from 19 focal nests plus adults from additional 24 nests that were collected from the same sites at the same time. Each locus had between 18 and 47 alleles represented in the sample of 148 individuals. All individuals were amplified twice independently at each locus and each author scored autoradiographs independently. Samples were re-amplified to resolve any equivocal scores. Genetic relatedness was estimated using the programme Relatedness version 5.08 (Queller and Goodnight 1989: (<http://www.gsoftnet.us/GSoft.html>)). Colonies were weighted equally and standard errors obtained by jack-knifing over nests. The software Kinship (Goodnight and Queller 1999: (<http://www.gsoftnet.us/GSoft.html>)) was used to determine whether pairs of nestmates were significantly more likely to have one relationship (e.g. sisters) than another (e.g. aunt–niece). Power was 92% (sister–niece analysis) or 98% (sister–cousin) at the alpha < 0.05 level.

Statistical analysis

Data were analysed using generalized linear modelling in the *R* statistical package (The R project for statistical

computing, version 2.0.0 for Macintosh; with reference to Crawley 2005). In the analysis of variables correlated with queue-jumping, explanatory variables tested were nest identity, group size, relatedness to nestmates, age difference to next oldest female, wing length, age rank and proportion of time spent off the nest. In all analyses we included females for which data were available for all explanatory variables and we began all analyses with all explanatory variables fitted. 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. Means+standard errors are reported.

Results

Removal of successive dominants

The removal of successive dominants in 2001 revealed a significant positive relationship between relative age and inheritance rank (Spearman's $\rho_{(0.05)}(n=69)=0.940$, $P < 0.001$; analysis including only individuals that could be unequivocally aged with respect to all of their nestmates) (Fig. 1). There was no evidence that body size or relatedness influenced dominance. Using generalised linear modelling with a binary y -variable (0=dominant, 1=non-dominant), there was no effect of wing length or relatedness to

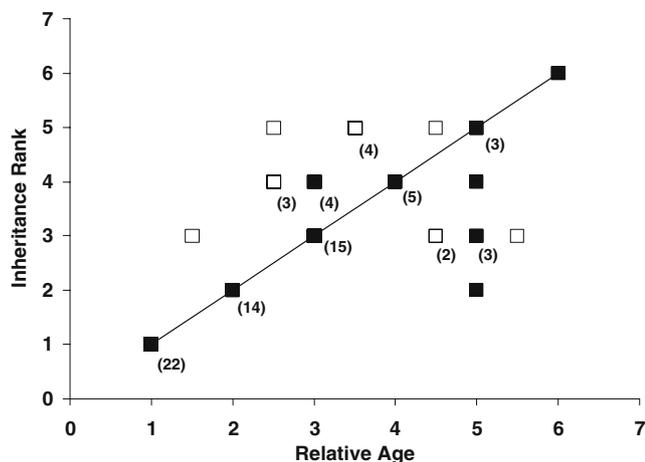


Fig. 1 Inheritance rank and relative age in *L. flavolineata*. The inheritance rank (IR) scale corresponds to the order of inheritance i.e. IR 1 individuals inherited dominance first, IR 2 individuals inherited dominance after the removal of the rank 1 and so on. Relative age (RA) 1 indicates the oldest individuals upon the nest to RA 7 who are the youngest. The line connects the individuals that obeyed the gerontocratic rule. Numbers indicate the sample sizes (where $n > 1$). Points below the line indicate the queue jumpers. Points above the line indicate the supplanted individuals. Open symbols are cases where the exact RA is unknown and are displaced by half an interval above their estimated age for greater clarity

nestmates but a significant effect of relative age ($P < 0.001$). Dominants present before any wasp removals were the largest females in only 6/22 groups. Group size averaged six females, so that this is approximately what would be expected by chance. Neither body size ($P=0.73$) nor genetic relatedness ($P=0.55$) was correlated with inheritance rank.

Of the 69 individuals that acceded to dominance and could be clearly aged, only 5 (7.2%) jumped the age-based queue. These 5 individuals inherited dominance ahead of between 1 and 3 (mean=2.0) older (supplanted) nestmates (Fig. 1). Queue jumpers supplanted females that were between 3 and 96 days older than them. Two additional queue jumpers could not be aged precisely, but each inherited dominance ahead of one older female. One further queue-jumping event may have occurred, but is equivocal because the putative queue jumper had joined the group concerned after being marked on a different nest. This female jumped the queue if her age is taken as the date she joined the group, but her actual birth date is unknown.

Natural queue-jumping events

Of the 37 dominants present on August 31, 2003, 5 (13.5%) were not the oldest female in their group. In each case, there was one non-dominant female that was older than the dominant. A further two cases were equivocal because they involved a wasp, which joined from the outside population to usurp the dominant position. This can be deemed as queue-jumping if age is taken as the date she joined the group. A further four queue jumpers were identified in 2002, these being females that inherited dominance naturally when previous dominants died or disappeared. Each of these females was the second oldest female in the group after the previous dominant died, yet became the new dominant.

Determinants of queue-jumping

To examine what factors might determine whether a female jumped the age-based queue in 2001, we used generalised linear modelling with a binary y -variable: 0=non-queue jumper, 1=queue jumper. Data were available for seven of the eight queue jumpers. The following explanatory variables had no significant effects on the y -variable: group size before any dominant removals ($P=0.68$); a female's average relatedness to her nestmates ($P=0.31$) and her wing length ($P=0.87$). A fourth variable, a female's age difference to the female just ahead of her in the queue was also non-significant ($P=0.12$) when tested using a reduced dataset comprising the 47 females (29 nests) for which precise age differences were available. Two factors did have significant effects on the y -variable: a female's rank before any dominant removals took place ($P=0.001$) and the

proportion of time the female spent off the nest during the pre-manipulation censuses ($P=0.01$). Time off the nest is a measure of helping effort, and low ranked helpers are known to work significantly harder than higher ranked helpers in *L. flavolineata* (Field et al. 2006). In the present analysis, females that were initially lower ranked and females that initially worked less hard after controlling for rank were significantly more likely than others to jump the queue.

Females did not appear to jump the queue because they were unrelated to their nestmates or because the females that they supplanted were unrelated. The average relatedness of queue jumpers to nestmates was 0.48 ± 0.12 ($n=7$) and supplanted females to nestmates was 0.52 ± 0.10 ($n=7$). The relatedness of queue jumpers to ‘normal’ (relative age=inheritance rank) nestmates was examined with regard to the hypothesis that queue jumpers may receive little opposition from nestmates if the nestmates are more closely related to the queue jumpers than to females that will be supplanted. The relatedness of normal nestmates to supplanted females (0.56 ± 0.08) was not significantly different from their relatedness to the queue jumpers (0.46 ± 0.11), ($t_{(0.05)}(n=7, \gamma)=0.727$, $P=0.48$) or to fellow normal nestmates (0.50 ± 0.15), ($t_{(0.05)}(n=7, \gamma)=-0.377$, $P=0.71$). Queue jumpers (wing-length= 4.3 ± 1.63) were not particularly large compared with non-queue jumpers in the general population (4.26 ± 0.39). Queue jumpers were larger than the individuals they supplanted in only 4/7 cases. The age difference between queue jumpers and those they supplanted varied widely (see Fig. 2).

Kinship analysis

The kinship analysis showed that five out of seven queue jumpers were significantly more likely to be sisters of the wasps they supplanted than nieces. The genotype of one

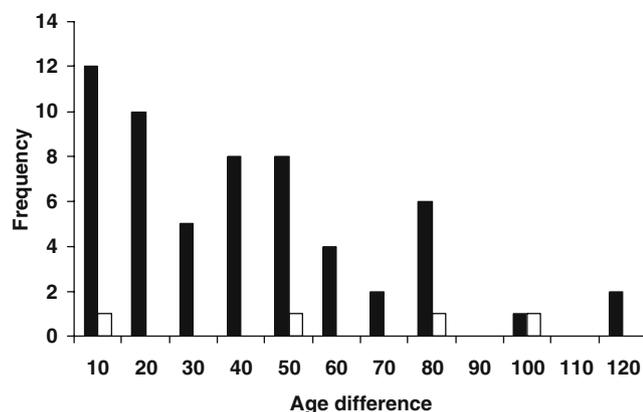


Fig. 2 Frequency histogram of differences in age (days) between each known age female and the next oldest in the queue for non-queue jumpers (black bars) and for queue jumpers to the oldest wasp supplanted (open bars)

queue jumper meant that she could have been either a sister or niece of the three older females that she supplanted. A sister relationship seems most likely for two of these supplanted females because they emerged as adults within a few days of the queue jumper on the same nest. The seventh (putative) queue jumper was the joiner mentioned above. It was unrelated to the individuals it may have supplanted. According to the kinship analysis, queue jumpers belonged to sibships of varying sizes having between zero and five sisters on the nests where they attained dominance.

Discussion

There was a significant correlation between relative age and inheritance rank in *L. flavolineata* (Fig. 1). The gerontocracy appeared to be stable with very few exceptions: only 13% of wasps jumped the age queue. The proportion of individuals that jumped the queue during experimental dominant removals in 2001 was very similar to the proportion observed on the un-manipulated nests in 2003. This suggests that experimental removals can provide meaningful data about the natural patterns of accession.

One explanation for the existence of a gerontocracy is that age is simply a convention for determining dominance. This begs the question, however, of why an age-based rule has apparently evolved in multiple lineages (Tsuji and Tsuji 2005). One possibility is that through age-based queuing, higher quality individuals are effectively selected to be dominants, if higher quality individuals are the most likely to survive long enough to inherit. There is currently no evidence that the correlation between age and rank in *L. flavolineata* reflects an underlying correlation between age and either fighting ability or some other aspect of female quality. All *L. flavolineata* helpers appear to have the potential to become egg-layers (Field and Foster 1999). Unlike some cooperatively breeding vertebrates in which individuals grow as they age, older (higher-ranked) *L. flavolineata* helpers are not larger than their younger, lower-ranked nestmates. High-ranked individuals are also no more closely related to their nestmates than low-ranked individuals. It is possible that older helpers are in better condition than younger ones because of preferential access to food or because older helpers forage less (Field et al. 2006). Even if this was the case, however, it provides only a proximate explanation for age-based inheritance, leaving unanswered the question of how older individuals gain such advantages. One advantage that age could potentially confer upon an individual is greater experience, and this remains to be investigated in *L. flavolineata*.

There is evidence that two types of age-based queuing occur in primitively eusocial Hymenoptera. In some taxa,

the death of the dominant leads to the oldest helper replacing her, whereas in other taxa it is one of the youngest helpers that is the replacement (Tsuiji and Tsuiji 2005). On the basis of an inclusive fitness model, Tsuiji and Tsuiji (2005) recently suggested that the occurrence of these two queuing mechanisms should depend on the expected life span of the group relative to the life span of the individuals. Where groups are short-lived, as in temperate eusocial insects, the oldest helper should replace the dominant. When groups far outlive individuals, however, the youngest helper should be the replacement. The phylogenetic position of hover wasps is currently controversial (Schmitz and Moritz 1998; Carpenter 2003) and they may provide an independent test of the prediction of Tsuiji and Tsuiji (2005). *L. flavolineata* nests potentially persist indefinitely. There is no absolute winter at our Malaysian study sites, so that brood rearing continues all year (Samuel 1987). Although not all *L. flavolineata* groups will outlive individual group members, especially if group size is small (Shreeves and Field 2002), the gerontocracy observed in *L. flavolineata* in which the oldest helper inherits the dominant position appears to contradict the prediction of Tsuiji and Tsuiji (2005). Tsuiji and Tsuiji (2005) note that there are other exceptions to their prediction.

One interesting property of a gerontocracy is that by helping, individuals avoid rearing offspring that will later compete with them for dominance. This is because each offspring will by definition join the queue at a lower rank than the helpers that raised it because it will be younger than them. In contrast, a queuing rule based on any other trait, such as body size, would lead to helpers sometimes rearing offspring with a superior trait to their own. Thus, they would be helping to rear competitors that could supersede them in the queue to dominance. Consequently, gerontocratic queuing could potentially promote the evolution of helping, although this requires more theoretical investigation and begs the question of why the youngest individual inherits in some taxa (M. Cant and J. Field, unpublished).

Although inheritance was mainly gerontocratic in *L. flavolineata*, a few individuals appeared to ‘cheat’ by not obeying the age rule. By jumping the queue, they accelerated their accession to an egg-laying position. They also avoided a significant amount of the foraging that a helper would normally undertake while waiting in the queue, during which there is an increased risk of mortality (Field et al. 1999; Cant and Field 2001; Shreeves and Field 2002). Although the small number of queue jumpers in our study meant that statistical tests had low power, we next discuss the available evidence as to why some individuals jump the queue.

Theoretically, females that are unrelated to their nestmates, such as wasps that join a group from the outside population, might have the most to gain from jumping the queue. Unrelated females cannot gain indirect fitness through helping and could therefore face the greatest selection pressure to jump the queue to dominance. In this study, 14% of the nests had joiners during the monitoring period (C. Bridge, unpublished) and indeed, two of the queue jumpers may have been unrelated to their nestmates. However, five out of the eight queue jumpers were sisters of the older individuals they supplanted. This suggests either that queue-jumping is not influenced by kinship or that it occurs for different reasons on different occasions. If queue-jumping involves aggression or fighting, it could be that individuals with a strong incentive to queue jump can do so only if they are larger than their nestmates. However, the queue jumpers in this study were not significantly different in body size from their nestmates. One possibility is that queue-jumping represents a frequency-dependent cheating strategy. A minority of females might somehow mimic cues correlated with age and so be mistaken for older females by their nestmates.

Rather than viewing it as ‘cheating’, an alternative interpretation of apparent queue-jumping is that the rules of inheritance are more complex than simple gerontocracy. There might be a second, subsidiary rule of inheritance such as “use relative age unless an older wasp is parasitised”. However, the impression gained from limited behavioural observations was that after queue jumpers achieved dominance, interactions between queue jumpers and rank two (supplanted) individuals were more aggressive than interactions between equivalent ranks upon nests in which queue-jumping had not taken place (unpublished data). This suggests that queue-jumping creates conflict and that such behaviour is breaking rather than adhering to a stable set of rules for inheritance.

In *L. flavolineata*, higher-ranked individuals work consistently less hard than lower-ranked individuals (Field et al. 2006). One interesting finding was that some future queue jumpers worked less hard than expected for their position in the queue. Reduced foraging should decrease the probability that a female dies before reaching the front of the queue and may be part of a cheating strategy. This finding also suggests that queue-jumping can occur well before a dominant dies, not necessarily at the moment of accession itself. It is unclear why females that were initially lower-ranked were more likely to jump the queue during experimental dominant removals. This pattern could be an artefact, in that lower-ranked females had more opportunities to queue-jump during our observations because a larger number of older females were experimentally removed in turn.

The study presented here raises a number of interesting questions concerning the mechanisms that *L. flavolineata* females use to determine their position in the queue. Cuticular hydrocarbon composition is known to change with age in some wasps (Panek et al. 2001; Lorenzi et al. 2004). In addition, because groups are small in *L. flavolineata*, it is conceivable that a focal female could learn the identities of the females present when she first reaches adulthood (see Tibbetts 2002): her queue position is then inversely related to the number of such individuals that remain alive. Studies that could identify and manipulate these cues could provide valuable insights into the queuing rules.

Acknowledgements We thank E. Almond, S. Brace, G. Shreeves and D. Stevens for the help with the fieldwork. Thanks also go to E. Hornett for the help with genotyping and K. Durai, H. Rosli and A. Sofian for their hospitality in Malaysia. A. Cronin kindly gave us access to the 2003 datasets. We thank E. Almond, E. Lucas, L. Zanette and A. Pomiankowski for the useful discussion and the Natural Environment Research Council for funding. The experiments conducted in this study comply with the current laws of the country in which they were performed.

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