

Males Exhibit Novel Relationships of Dominance with Nest Departure in the Social Paper Wasp *Mischocyttarus mastigophorus* (Hymenoptera: Vespidae)

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Abstract

In many animal societies, an individual's opportunities to reproduce correspond to their position in a dominance hierarchy. In primitively eusocial paper wasps, female social dominance and direct reproduction are positively associated with taking food from nest mates, but both negatively correlate with foraging flights. Female paper wasps reproduce by laying eggs in their nest, while males reproduce by leaving the nest to copulate. Males of *Mischocyttarus mastigophorus* are unusual because they reside on their natal nests for prolonged periods, and males direct aggression towards female nestmates. *Mischocyttarus mastigophorus* males provide an opportunity to further analyse the relationships between dominance, nutrition and nest departure. We found males' rates of social aggression, food taking behaviour, and rates of nest departure were positively correlated. Furthermore, males that initiated aggression at younger ages also began flying earlier, and males engaged in all three behaviours at younger ages than females. Male social aggression may lead to nutrient acquisition, which enable males to depart from the nest. We hypothesise that male nest departure could be adaptive if it increases male mating opportunities. This could account for the positive relationship between dominance and nest departure for males.

Introduction

Variation in female fecundity is often affected by differential access to the resources that support costly offspring production (Wade & Schneider 1992; Bridges & Heppell 1996; Reznick et al. 1996; Bentley 1999). Easy access to food leads to earlier onsets of fertility (e.g. human menarche: Bentley 1999), and well-fed females have increased numbers of progeny and enhanced offspring survivorship (Qian & Chia 1991). For insects, high nutritional stores can amplify ovary development and increase clutch and egg size (Blanckenhorn 1991; Fox 1993; Bridges & Heppell 1996; Hartsfelder et al. 2006). For social species, competition among group mates dictates access to food (Wheeler 1986; Markiewicz & O'Donnell

2001; Vervaecke et al. 2005). Dominant animals can exploit subordinates' foraging effort, and in a number of taxa females employ agonistic interactions to obtain food from group mates (birds: Lendvai et al. 2006; crustaceans: Fero et al. 2007; insects: Markiewicz & O'Donnell 2001; Molina & O'Donnell 2008). Aggression may additionally induce departure to forage for food, and dispersal from the group, in subordinates (Tacha 1981; O'Donnell 1998; Pilastro et al. 2003; Russell et al. 2003; Scott & Lockard 2006).

Females in primitively eusocial Hymenoptera provide excellent examples of the relationship of aggression with fecundity (e.g. independent founding paper wasps: West-Eberhard 1969; Free et al. 1992; O'Donnell 1998; Pardi 1948; Röseler 1991). Social

aggression directs nutrients away from foraging females and towards their dominant nestmates, and limits foragers' fecundity (Reeve 1991). Dominant females avoid off nest behaviours, such as foraging, possibly because of risks of predation and the exceptionally high energetic costs of hymenopteran flight, which may deplete their nutritional stores (Weis-Fogh 1973; Ellington 1991). Foraging by paper wasp queens drops steeply after workers emerge or cofoundresses join the colony (Itô 1983; Pratt 1989; Reeve 1991). Similar patterns are observed in the dominant workers that are most likely to supercede their queens (paper wasps: Premnath et al. 1996; Molina & O'Donnell 2009; ants: Heinze & Oberstadt 1999). Reproductive females in more advanced social species (e.g. ants, honey bees and swarm founding wasps) are largely nestbound after their mating flights, which typically occur during a brief period in early adulthood (Keller 1998; Strassmann 2001; Tapp & Page 2001). Female reproduction in many social Hymenoptera therefore appears to require a primarily on-nest life style, both to maintain the physiological capacity for reproduction, and to suppress reproductive competitors.

In contrast to social insect females, male reproductive strategies generally require extensive travel to find and copulate with unrelated females (Andersson 1994; Birkhead 2000). Social hymenopteran males rarely reproduce on their natal nest (West-Eberhard 1969; Litte 1979; Gadagkar & Joshi 1984; Giannotti 2004; but see O'Donnell 1994). Males generally depart from their natal nests quickly to secure mating opportunities with non-sibling females (see Strassmann 2001 for review; bees: Larsson 1991; ants: Hölldobler & Wilson 1990; Ruano & Tinaut 2005; wasps: Jeanne 1972; Beani 1996; Tindo et al. 1997). Once they depart the natal nest, males of many species do not return (Boomsma et al. 2005; O'Donnell & Beshers 2004). Dominant female group mates evict males in many social taxa (Gauthreaux 1978; O'Donnell 1999), because males contribute little labour to their colonies (Hölldobler & Wilson 1990; O'Donnell 1995, 1999).

Unlike males of most social Hymenoptera, adult male *Mischocyttarus mastigophorus* paperwasps return to and reside on their natal nests daily for at least several weeks. The males spend several hours each day away from the nest, presumably to attend mating aggregations (Strassmann 2001), but they return daily and spend the night on their nests (O'Donnell 1999).

Furthermore, unlike most Hymenopteran males (Gauthreaux 1978; Starks & Poe 1997), the males in

this species are dominant over females on their natal nest, including the queen (O'Donnell 1999). For both female and male *M. mastigophorus*, dominant individuals take most of the food brought to the nest by foragers (O'Donnell 1998, 1999).

Male *M. mastigophorus* provide an excellent and unusual opportunity to test the generality of associations between dominance, nutrition and nest departure in primitively eusocial species. We examined cross-sectional and developmental patterns of male aggression and nest departure. We measured rates of giving aggression, taking food from foragers, and departures from the nest. It is important to note that aggression and food taking are both negatively associated with nest departure in *M. mastigophorus* females (O'Donnell 1998; Markiewicz & O'Donnell 2001). We expected giving aggression and taking food to developmentally precede flight, to prepare males physiologically for costly off-nest behaviours. To test these predictions, we tracked individual male and female behavioural development, and then we quantified developmental differences between the sexes.

Materials and Methods

Study Site and Subject Colonies

We collected data from 27 Jul. to 7 Sept. 2006 from five post-worker emergence *M. mastigophorus* colonies. *Mischocyttarus mastigophorus* colonies are founded and males are present throughout the year at our field site in Monteverde, Costa Rica (10°18'N; 84°49'W; O'Donnell & Joyce 2001; S.O'D., pers. obs.). We observed the nests *in situ* in Monteverde (O'Donnell 1998, 1999; Markiewicz & O'Donnell 2001; Molina & O'Donnell 2008). We individually marked all adult resident wasps on the nests with paint pens 1–2 d before observations began and excluded them from the analyses.

To obtain known-age subjects, newly emerged wasps ($n = 59$, $n = 10$ – 14 per subject nest) were captured, anaesthetised with ether, marked with paint pens, and returned to their nests. We included only these known-age males ($n = 16$) and females ($n = 76$) in the analyses. Males were identified by their distinctive facial markings and elongate antennae (O'Donnell 1999; O'Donnell & Joyce 2001). To increase our sample size of known-age wasps, we also introduced adults ($n = 33$; $n = 5$ – 7 per subject nest) that emerged from source combs of other nearby colonies. We maintained source combs in plastic containers in the laboratory. We

marked wasps from these combs on the day of adult emergence and introduced them onto observation nests. As in other social Hymenoptera, newly emerged *M. mastigophorus* adults are accepted into foreign colonies (Bell et al. 1974; Jeanne et al. 1988; O'Donnell & Jeanne 1993; Molina & O'Donnell 2008).

Behavioural Data and Subject Collection

We observed each colony every 3 d, except that occasional observation days were skipped because of heavy rainfall. The order of observing colonies was not altered. For the first 2 d of each 3 d observation cycle, behavioural data were collected on two colonies per day (day 1: colonies A and B; day 2: colonies C and D). Behavioural data were collected continuously for 3 h in the morning (1.5 h per colony), between 0700 h and 1000 h local time, and for 2 h in the afternoon (1 h per colony), between 1200 h and 1400 h. On the third day, behavioural data were collected on one colony (colony G) in the morning for 1.5 h between 0700 h and 1000 h local time and for 1 h in the afternoon, between 1200 h and 1400 h. We observed colonies on a total of 11–14 d each over the course of 35–42 d.

We collected behavioural data using a portable tape cassette recorder while standing on an extension ladder 0.5 m from the nest, facing the cell openings. All occurrences of the following behavioural acts were noted for all individuals present: arrivals and departures from the nest with time to the nearest minute, giving aggression (chasing and biting nestmates), receiving aggression and taking food from incoming foragers (see Itô 1984; O'Donnell 1998, 1999 for descriptions of *Mischocyttarus* behaviour). We used the timing of arrivals and departures to calculate time spent on the nest for each wasp. Queens were identified based on observations of egg laying; one female per colony laid eggs during the study. Colonies were collected in evening of the last behavioural observation day. Ages of wasps collected at the end of the study ($N = 73$; surviving males $n = 13$, surviving females $n = 60$) ranged from 1 to 46 d.

Statistical Analyses

We accounted for colony identity in all analyses. Behavioural data that did not meet assumptions of parametric tests (e.g. unequal variances) were square-root transformed (Pedhazuer 1982).

To test for developmental ordering of behaviours, we used the age (in days) at first observed performance for key behaviours (i.e. departures, giving and receiving aggression and taking food from foragers) as an indicator of the onset of activity (O'Donnell 2003; Giray et al. 2005). We analysed differences in the age at first performance of behaviours using survival analysis implemented in SPSS 14, 2007. Survival analysis provides unbiased estimates of time distribution parameters by including censored values (Pyke & Thompson 1986); wasps that had not performed the response behaviour before the study ended were included in the survival analysis as censored values. We used the nonparametric Wilcoxon test to compare age of onset among different behaviours within sexes, and we performed Cox regression analyses to examine sex-related differences in development. We applied a Bonferroni correction for inflated type I error rates when we made multiple pairwise comparisons within an analysis (Pedhazuer 1982).

For each wasp, we also calculated daily rates of behaviour (frequency/h spent on nest) for giving aggression and taking food from incoming foragers, and we calculated daily rates of departures from the nest (frequency/observation hour). We used multiple regression analyses to test whether rates of performance changed with age (Pedhazuer 1982). We also tested for individual differences in the pattern of change in behavioural rates with age by examining the individual*age interaction terms for each behaviour (Pedhazuer 1982). All individuals were included in these analyses, including those that disappeared before the end of the study.

Results

Correlations Among Behavioural Acts

After accounting for age effects, total rates of departures and giving aggression were positively correlated for males (Fig. 1a; $r = 0.77$, $df = 10$, $p = 0.004$). Total rate of taking food was also positively associated with rates of departures (Fig. 1b; $r = 0.59$, $df = 10$, $p = 0.04$) and of giving aggression (Fig. 1c; $r = 0.78$, $df = 10$, $p = 0.003$). Like males, females showed a positive association between rates of taking food and giving aggression (Fig. 1f; $r = 0.29$, $df = 68$, $p < 0.01$). However, in contrast to the males, there was a non-significant trend towards a negative correlation between total rates of departures and giving aggression for females (Fig. 1d; $r = -0.21$, $df = 68$, $p = 0.08$). Females' total rates of

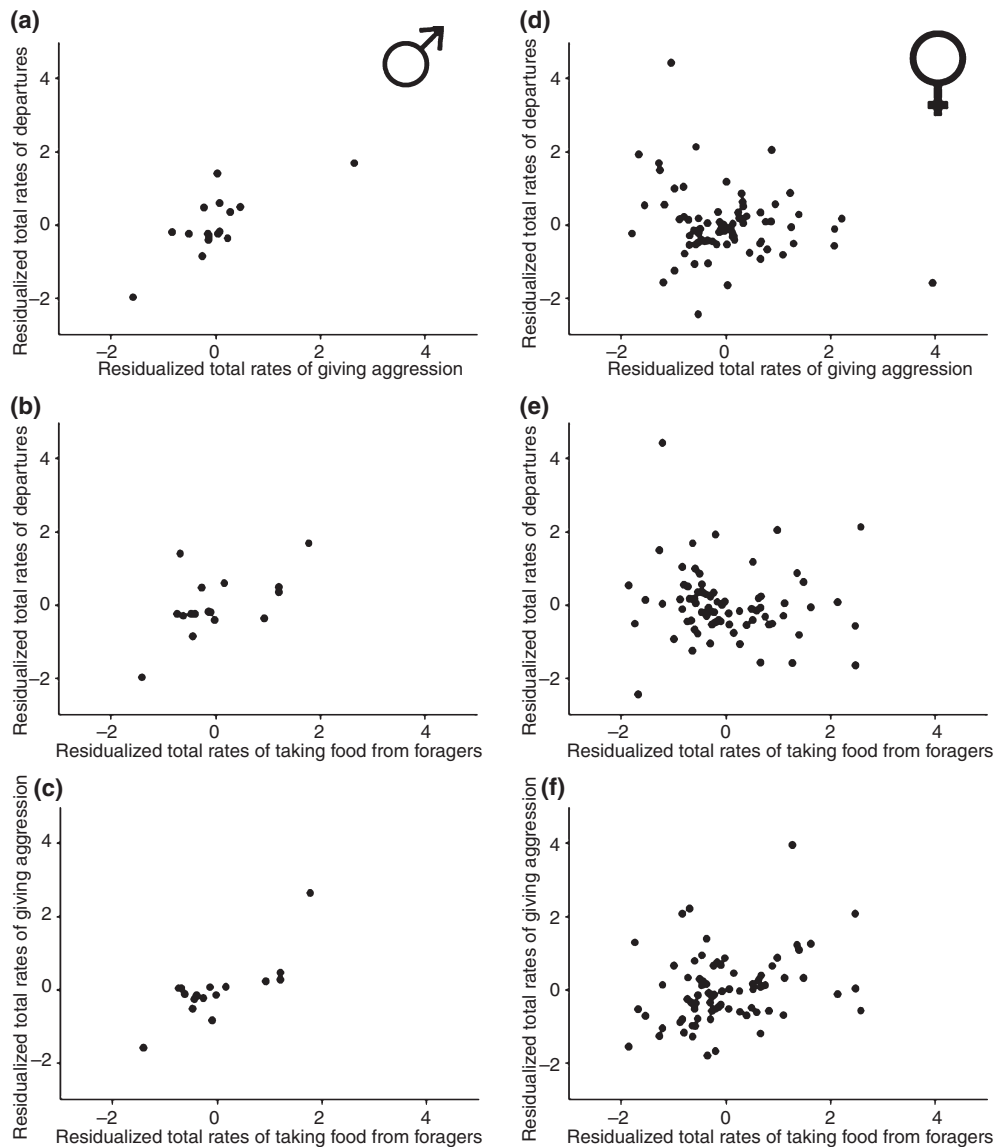


Fig. 1: Partial correlation plots depicting relationships between rates of performing key behaviours for males and females, after accounting for the effects of age and inter-colony variation.

departures and taking food were not significantly related to each other (Fig. 1e; $r = -0.09$, $df = 68$, $p = 0.47$).

As previously observed (O'Donnell 1999), males obtained food from incoming foragers more frequently than their female nestmates ($t_{71} = 5.22$, $p < 0.0001$). The daily number of male departures was positively correlated with the daily number of foragers arriving with food ($r = 0.44$, $df = 47$, $p = 0.002$). Males rarely received aggression. Only three males in our study received aggression from female nestmates, and each received aggression on a single occasion.

Patterns of Male Behavioural Development

The age of first performance differed significantly among giving aggression, taking food and foraging for males (Survival analysis Wilcoxon test: $\chi^2_4 = 12.67$, $p = 0.002$). All except one male began to give aggression and take food from foragers on the same day (median age of first performance = 2 d). Males began to take food and give aggression earlier than they began to leave the nest (median age for nest departures = 5 d; Wilcoxon $\chi^2_1 = 2.54$, $p = 0.01$). Males that gave aggression at younger ages also departed the nest at younger ages (Wilcoxon $\chi^2_1 = -2.38$, $p = 0.02$).

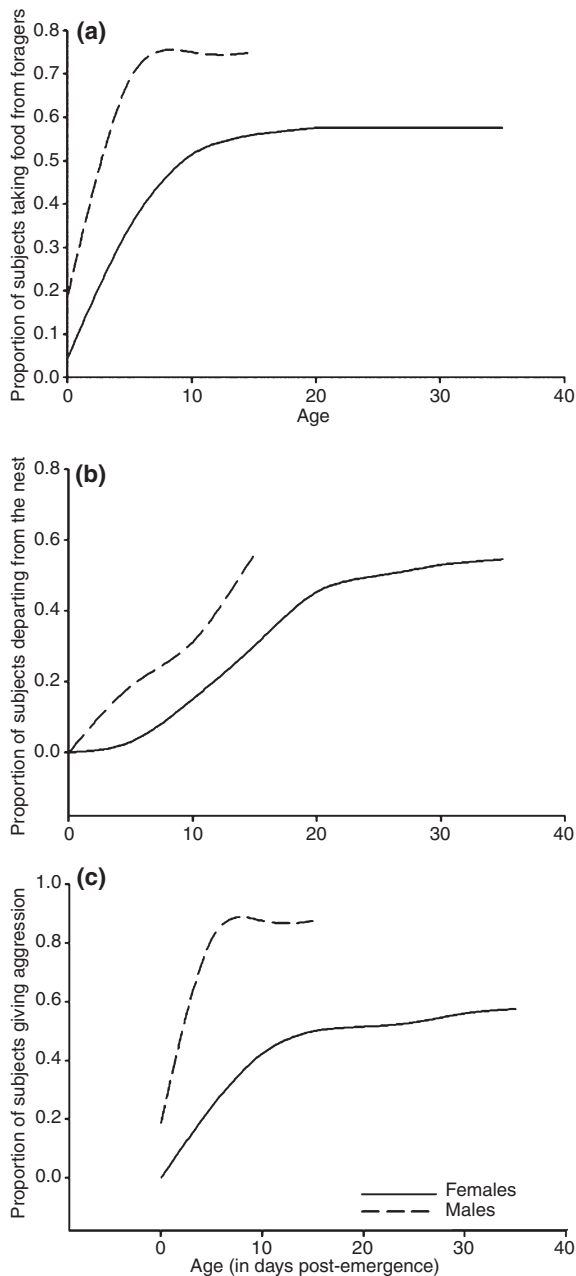


Fig. 2: Cumulative curves depicting sex differences in the age at onsets for taking food from foragers, giving aggression and departing from the nest. Dashed lines denote male development and solid lines female development.

Sex Differences in Behavioural Development

Males and females differed in the ages of onset for performing all behaviours. Males began performing most of the behaviours we selected for analysis earlier than females (Fig. 2; taking food – $\chi^2_1 = 22.25$, $p < 0.0001$; directing aggression – $\chi^2_1 = 66.58$, $p <$

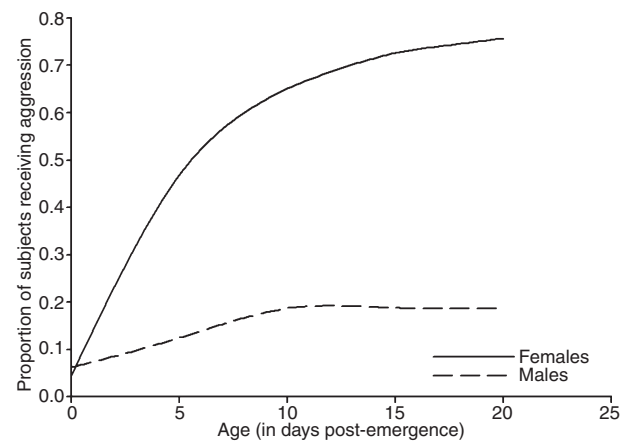


Fig. 3: Cumulative curves depicting sex differences in the age at onset of receiving aggression. Dashed lines denote male development and solid lines female development.

0.0001; departing from the nest – $\chi^2_1 = 27.34$, $p < 0.0001$). In contrast, females began to receive aggression earlier than males (Fig. 3; note that most males never received aggression, and they were included as censored values in this analysis; $\chi^2_1 = 10.96$, $p = 0.001$).

Discussion

Our data provide evidence for sex-based differences in *M. mastigophorus* behavioural development. Males began to depart the nest at younger ages than females. Males performed on nest activities that may prepare them for flight, such as giving aggression and taking food, earlier than females. In contrast, female workers, who generally leave the nest to forage in response to social aggression from nestmates (Reeve 1991; Beshers et al. 2001; O'Donnell 2003), began to receive aggression at earlier ages than males.

In this study, we tested the generality of social dominance as a mechanism to augment nutritional reserves in social animals. Dominant animals in social species often monopolise the majority of available food by defending clumped resources and attacking nearby subordinates (Klaassen et al. 2006; Scott & Lockard 2006; Taillon & Cote 2007) and by inducing foraging behaviour in subordinates (David et al. 2007). Although males and females often employ disparate reproductive strategies, sufficient nutrient stores affect fecundity throughout the animal kingdom (see Allen & Ullrey 2004 for review). For females, nutrition can influence the onset of reproductive capacity (Luquet & Watanabe 1986;

Bentley 1999), the number, size and survivorship of offspring (Qian & Chia 1991) and certain maternal behaviours (Wade & Schneider 1992). Male nutrition can influence fertilization success (Brown 1994; Delise & Hardy 1997). Male *M. mastigophorus* are unusual among social Hymenoptera because they are dominant over their female nestmates (O'Donnell 1999; also see *Mischocyttarus collarellus*, Smith 2005). We found that male's (but not female's) rates of nest departure were positively associated with their rates of giving aggression and taking food. The onset of giving aggression and taking food preceded the onset of nest departure for males.

Social hymenopteran males perform few of the tasks necessary to support colony productivity, and males apparently never forage for food or building materials (O'Donnell 1995, 1999). In many species, social aggression is directed at males to evoke permanent departure and mating away from the nest (Litte 1979, 1981; Starks & Poe 1997). In *M. mastigophorus*, however, males do not permanently leave their nests, and they rarely receive aggression from nestmates (male or female; O'Donnell 1999). Instead, males are socially dominant, directing aggression towards females at high rates and taking the majority of food from incoming foragers (O'Donnell 1999). O'Donnell (1999) suggested that males' social dominance in *M. mastigophorus* could function to enhance male longevity. Our findings suggest that social dominance and food taking behaviour have an additional function: augmenting time away from the nest. Male aggression was associated with earlier onset of departure from the nest and positively correlated with nest departure frequency. Conversely, female dominance is associated with later onsets of departure from the nest (Molina & O'Donnell 2008). After they have made their mating flights, females increase their fecundity by laying eggs in their nests (Strassmann 2001). For females who benefit from remaining and laying eggs on the nest, dominance suppresses competing females' reproductive development and removes them from oviposition sites by inducing foraging (Reeve 1991).

The fact that receiving aggression is associated with departure only for females at first seems surprising, given the high energetic and mortality costs of flight away from the nest (Rothe & Nachtigall 1989; Nation 2002). We propose that the sex differences we observed could be adaptive: the opposite relationship between dominance and nest departure for males and females is consistent with the hypothesis that members of each sex are behaving so as to maximise opportunities for obtaining direct

reproduction. Nest departure is favourable to male fecundity, and costly to female fecundity (mating flights aside). Colonies may profit from male dominance behaviour and food consumption, if males departing the nest acquire a greater number of successful fertilizations. However, males consume food resources. Because males rarely perform labour (e.g. foraging, broodcare; Cameron 1985; O'Donnell 1995, 1999; this study), male dominance entails costs for their colonies. Female siblings in other species may evict males because of these costs (e.g. Gauthreaux 1978). Male removal experiments and other studies evaluating the benefits and costs of male presence on nests would be useful in determining the adaptive value of male dominance in *M. mastigophorus*.

Future studies are needed to reveal explicitly what *M. mastigophorus* males do while they are away from their nests. Males are known to participate in off-nest aggregations that are visited by females, and these may represent mating aggregations (O'Donnell 1999; S.O'D. pers. obs.). It is possible that there are greater energetic costs attached to leaving the nest for males, perhaps because of greater distances travelled, additional time spent in flight, or costly courtship and copulation. This could enhance males' need to consume large amounts of food to fuel their flights. As an alternative or in addition to mating opportunities, males may leave the nest to obtain food for their own consumption. This seems unlikely given the available resources on the nest, and the fact that males intake the majority of the food that is brought to the nest (O'Donnell 1999, this study). If males left the nest to forage, they should also depart from the nest more frequently when there are limited resources (e.g. fewer arrivals with food). In contrast, we found that males departed more frequently when there was more food available. Competition with nest mates may restrict individual males' access to resources when they are on the nest. Studies determining the proportions of departures dedicated to mating vs. food foraging would distinguish mating vs. nutritional payoffs of male nest departure.

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