May 2009

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ABSTRACT

Males of independent founding hymenoptera contribute little to the nest by not foraging for food or feeding larvae. Males are a potential cost to the nest because they consume resources and are not used for reproduction, but males of *Myschocyttarus mastigophorus* can be found on the nest year. To investigate if the behavior of females changes when the males are not present, baseline behaviors of both males and females were recorded for four nests *M. mastigophorus*, then the males were removed and observations continued. Baseline behaviors indicate that females departed ($t = 2.33$) and arrived ($t = 2.81$). Departures increased after the males were removed ($t = 2.33$, all $p < 0.10$) and there was a trend for females to arrive more frequently ($t = 1.67$, $p = 0.14$). Females possibly increased these behaviors to forage while the males are not present so the males cannot take food away from the females. It is possible that the males are present year round purely for reproduction with non-sibling females.

RESUMEN

Machos de himenóptera contribuyen muy poco a la colonia ya que no cumplen ninguna función de forrajeo o alimentación de larvas. Los machos son un posible costo para el nido debido a que consumen recursos y no son utilizados para la reproducción, pero los machos de *Myschocyttarus mastigophorus* pueden ser encontrados en los nidos aún un año después. Para investigar si el comportamiento de las hembras cambia cuando los machos no están presentes, datos basales del comportamiento tanto de machos como de hembras fueron tomados para cuatro nidos, luego los machos se removieron y se continuaron las observaciones. Estos datos indican que las hembras se marchan (t= 2.33) y arriban (t= 2.81). Las partidas aumentan después de que los machos se removieron ($t = 2.33$, all $p < 0.10$) y hay una tendencia a arribar más frecuentemente ($t = 1.67$, $p = 0.14$). Las hembras posiblemente aumentan el comportamiento de forrajeo cuando los machos no están presentes, así los machos no pueden tomar alimento del que transportan las hembras. Es posible que los machos que estén presentes todo el año para reproducirse con hembras no relacionadas genéticamente

INTRODUCTION

Independent-founding eusocial wasps exhibit a dominance hierarchy. This linear hierarchy is used not only for the foundress to prevent lower females from reproducing, but also to make them do nest maintenance activities, such as foraging (de Souza 2008). Females of *Mischocyttarus mastigophorus* perform the majority of the tasks associated with colony maintenance, including foraging, nest building, and feeding larvae. Males usually do not participate in these tasks, or participate in very low rates (O'Donnell 1995). Giannotti (2004) found the behavior "remaining immobile on the nest" comprised more than 82 percent of all observed behaviors in males of *Polistes fuscatus*, another independent founding Vespidae. Males performing behaviors relating to colony maintenance was scarce, including giving alarm 4.8% of the time and feeding larvae

0.8% of the time (Giancotti 2004). Males of both *Polistes fuscatus* and *Mischocyttarus cerberus* also do not participate in colony defense against predators (Judd 1999; Togni & Giannotti 2006).

Males of most social Hymenoptera species depart their natal nests to mate with unrelated females and do not return (O'Donnell & Beshers 2004; Strassman 2001). Males of *M. mastigophrous,* however, return to the natal colony after mating and remain on the nest for up to several weeks (Jeanne 1972; O'Donnell 1999; West-Eberhard 1969). Unlike other Vespidae, males are aggressive to the females on their natal nests, and the females respond to male aggression with submissive behaviors such as crouching, fleeing and departing the nest (O'Donnell 1999). These aggressive, seemingly dominance behaviors may be related to the observation that males do not forage, and rely on female foragers for food.

Since the males consume resources, but do not contribute to nest maintenance activities such as foraging and feed larvae, it is possible that they are significant cost to the nest (O'Donnell 1999). This is especially true since they remain on their natal nests longer than males of other social hymenoptera. As the ratio of males to working females increases, workers cannot bring enough food to support the entire colony, which can lead to colony decline (Jeanne 1980). Males may be an even greater cost during the dry season, when the colony already has reduced colony growth due to low prey abundance (O'Donnell 2000).

This sex-biased workload and consumption of resources provides interesting questions as to the function of males on the nest. They do no reproduce with females on their natal nests, and can be found on the nests all times of the year and during all stages of colony development (O'Donnell 1999). This constant male presence suggests that they may have some specific role in the nest other than reproduction, even though they appear to contribute little.

There is an overall lack of knowledge of male behavior and function in paper wasps, especially tropical species (O'Donnell 1999). The purpose of this study is to investigate if the females change their behavior after the males are removed from the nest. The results of this study will give more insight into the importance, if any, of producing males that remain on their natal nest. If males have a role in the nest other than reproduction, females may adjust their actions to compensate for the sudden male absence.

METHODS

Procedure

Observations took place at the Monteverde Cloud Forest Reserve (MVCFR) in Monteverde, Costa Rica. Four nests of *Mischocyattarus mastigophorus* were located on the rafters of buildings within the MVCFR complex (n = 5 to 8 individuals per nest) from 20 April 2009 to 3 May 2009. All observations took place between 0930 and 1200 for morning observations, and 1230 and 1500 for afternoon observations, with one colony observed at a time. The following methodology was used for each colony sampled. One day of baseline behavioral observations was taken with two hours of observation in the morning and two hours in the afternoon. At sunset (approximately 1800 local time) the

day of baseline behavioral observation, males were removed from the nest after observations were completed. Males were distinguished from females by their long, filamentous antennae and white faces (O'Donnell 1999). After males were removed, behavioral observations were continued the next day, with two hours of observations in the morning and two hours in the afternoon.

Behavioral Observations

The researcher stood on a ladder directly in front of the nest, within 0.5 meters. A hand held tape recorder was used to record all observations for each two hour block of time. Observed behaviors included nest maintenance tasks, social interactions, flying departures and arrivals, transfers of food and building materials, chasing, biting, and displacing (O'Donnell 1999). Recordings were transcribed and quantified at a later date for statistical analysis.

Statistical Analysis

A sum of all behaviors from each nest was transcribed from the tape recordings and then transformed into rate per individual per hour for each behavior. The average rate per individual per hour for each behavior was used in independent sample t-tests for comparing differences in male and female behaviors and paired t-tests for comparing female behavior after the males were removed to baseline behavior.

RESULTS

Primary Findings

During baseline observations, females departed the nest more than males (t = 2.33, p = 0.058)(see Fig. 1). Females also arrived on the nest more than males, (t = 2.81, p = 0.03; Fig. 1). There was also a trend for females to arrive on the nest with food more frequently than males (t = 1.67, p = 0.14; Fig. 1). Females departed the nest more after the males were removed than when the males were present (t = 2.33, p = 0.10; Fig. 1). Similarly, there was a trend for females to arrive on the nest at a higher rate when the males were absent compared to when the males were present (t = 2.35, p = 0.13; Fig. 1). While the rate of females arriving on the nest with food decreased after the males were removed, this decrease was insignificant (t = 0.84, p = 0.57; Fig. 1).

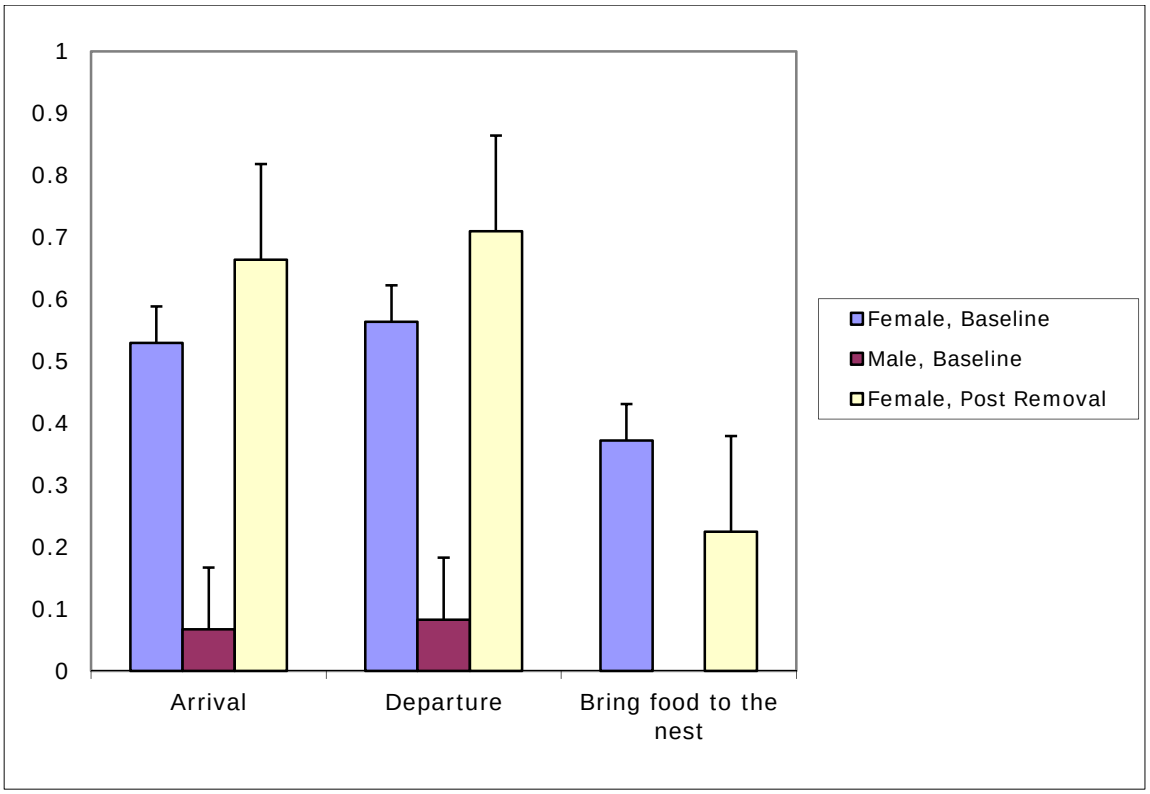

FIGURE 1. Comparison of female behavior, male behaviors, and females, and female behavior after the males are removed from the nest. Females arrived and departed the nest significantly more than males. Female departures increased after the males were removed. Females also put their head in a cell significantly more than males, but this data was excluded from the analysis

Other Observations

The most commonly observed behavior was when a female put her head in a cell. Females performed this behavior at a significantly higher rate than males (t = 3.47, p = 0.01; Fig. 2). The rate of this behavior decreased in females after the males were removed, but this change was insignificant (t = 0.43, p = 0.69). However, this behavior was excluded from the analysis because it is not clear what task the wasps were performing. When an individual sticks its head in a cell, the individual could be feeding larvae, or the larvae could be feeding the individual (Y. Molina, pers. comm.). Since it was important to determine exactly what task the male and female wasps were performing to determine if behavior was changing post-male removal, this behavior was excluded from the analysis.

Another interesting observation was the number of individuals on each nest. Of the four nests included in this analysis, there was a range of five to eight total individuals per nest, which was much lower than found by previous studies, some of which occurred at the same location (Table 1). However, the percent composition of males on the nest

was very similar. This stud found males comprised an average of 46% of individuals on the nest, while O'Donnell (1999) found males comprised 41%.

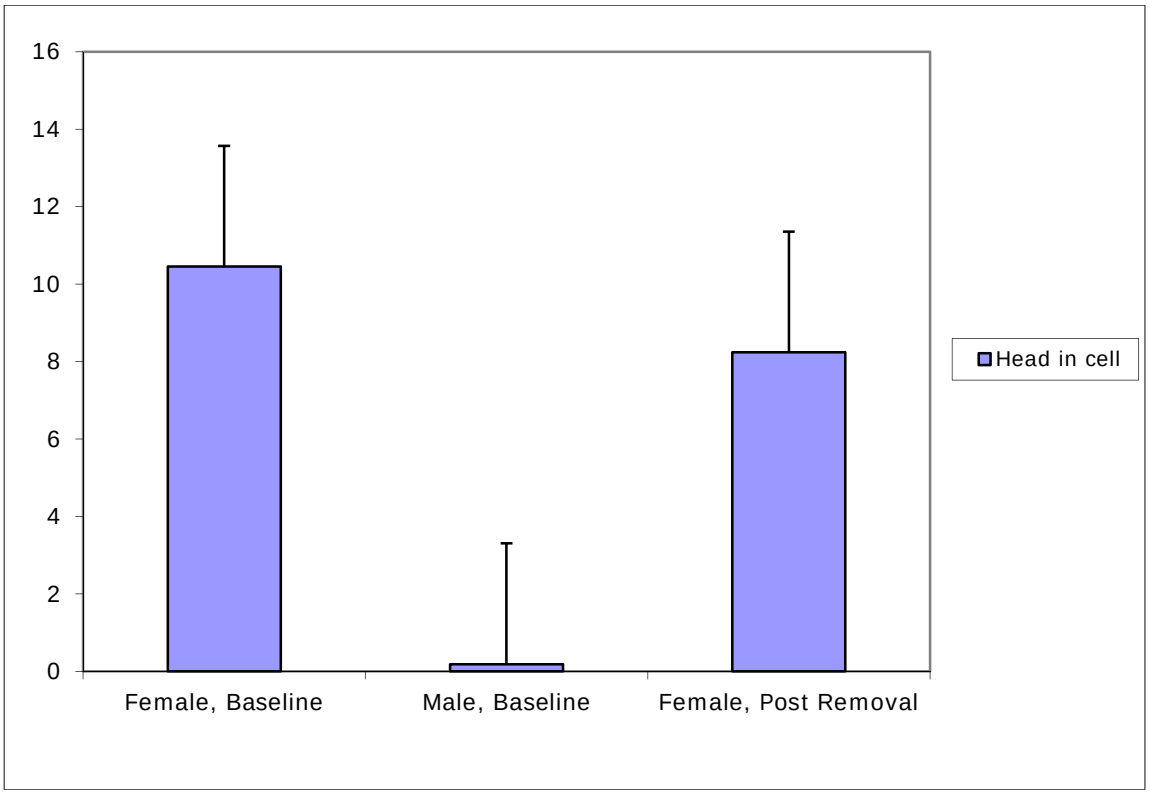

FIGURE 2. Comparison of the rates of individuals putting heads in cell for female baseline, male baseline, and female after the males were removed.

TABLE 1. *Comparison of the number and composition individuals on the nest with previous studies. While the total number of individuals has declined in comparison to previous years, the percent composition of males on the nest is similar.*

Study	Location in Costa Rica	Species	Wasps per nest	Avg. number of wasps per nest	Avg. % composition of males	% Range of males per nest
O'Donnell, 1999	Monteverde	*M. mastigophorus*	2 – 128	23.9	41	25 - 58
O'Donnell, et al, 2007	Monteverde	*M. mastigophorus*	7 – 13	9.9	----------	----------
Feit, 2009	Monteverde	*M. mastigophorus*	5 – 8	6.5	46	20 - 63

DISCUSSION

Females participated in behaviors at a higher rate than males for departures, arrivals, and bringing food to the nest. This sex-biased division of labor supports results found in other studies that females perform colony maintenance behaviors at a higher rate the males (Judd 1999; Giannotti 2004; O'Donnell 1995; Togni & Giannotti 2006). After the males were removed from the nest female behavior increased in arrivals and departures, but bringing food to the nest decreased after the males were removed compared to when the males were present.

Perhaps the females increased departures and arrivals to forage. If there are no males on the nest to take the food, then there is more for the other females and the larvae. If the females are taking advantage of the absence of males to increase foraging, this is perhaps a clue that the males are a cost to the nest. However, females brought less food after the males were removed than when the males were present. This does not mean they are foraging less, but rather that with the males on the nest they do not need to bring as much food back because the male will not take any of it away.

Another explanation for the changes in behavior seen after males were removed is that these changes are normal for females while the males are gone, since males usually leave during the day to search for mates (Jeanne 1980). It is possible that females always increase foraging while the males are gone so the males cannot steal food away from them when the females arrive on the nest with food. With the males being removed permanently in this study, they were gone for an extended period of time compared to the baseline observations. The removal allowed the females to continue increasing the arrivals and departures throughout observations. While explanations are varied as to reasons why females may change behavior when the males are removed, they clearly do change their behavior, indicating some underlying mechanism of male presence on the nest.

A second question of this study is why are there males on the nest year round if they contribute little to the nest? Related to this question is the observation that the male composition of males on the nest in this study was very similar to male nest composition in previous studies. It is possible that ~41% may be the optimal percentage of males to maximize fitness. Since males are haploid, they are more related to the foundress (their mother, 100% related) than diploid sisters are to the foundress (average of 75% related). Therefore the foundress increases her fitness, via genetics, when her sons reproduce when compared to producing sisters. Perhaps *M. mastigophorus* does not have a single breeding season, so females produce males year round to maximize their fitness. However, it is not beneficial to produce as many males as possible because males only consume resources from the nest and contribute little, which is a possible cost to the nest. It is possible that the male composition observed in this study and in previous studies on the nest is stable and maximizes the fitness of the foundress without sacrificing the cost of maintaining the nest via consumption of resources.

Despite the hypotheses being presented, the function of having males on the nest year round is still unknown. If the males do not perform activities that benefit the nest (such as foraging for food and feeding larvae) and if females increase foraging while the males are absent so they do not steal the food, then it would seemly costly to the nest to have them present year round. This study was conducted at the end of the dry season

when colonies should be experiencing a decline in growth (O'Donnell 2000). However, there were males present on each nest found despite there being a small amount of females. This observation supports the hypothesis that males increase fitness of the foundress because of their haplodiploidy.

Future studies could repeat this one, increasing the number of nests, since this study only included four. This study could also be extended throughout the year since many studies conduct observations between May and September. This could confirm the changes behaviors, as well as possibly show other changes in behavior. This study could also be repeated with marking individuals and seeing if the rates of individual females increases or decreases differently than other individuals. To test if the hypothesis that females increase behaviors normally while males are not on the nest, a study could compare the behavior of females while males are present versus absent, except without manipulation of removing the males. This would show if females do try to prevent males from taking food by foraging when they are absent. Another important area of investigation is continuing to study the role of the males on the nest, since their role other than reproduction is still unknown.

Overall, there were marked changes in female behavior after the males were removed from the nest. The rate of females arriving and departing increased when the males were not present. This possibly indicates that females are trying to compensate for males using resources by increasing foraging while the males are absent so the males cannot take food that could be used for the females and the larvae. On the other hand, it may also be beneficial to have males on the nest year round because their haplodiploidy increases the fitness of the foundress when her sons mate with females from other nests. Despite these hypotheses, the role of the male on his natal colony is still unknown.

ACKNOWLEDGEMENTS

A big thank you to Anjali Kumar for all her help and support in the planning execution of this project, as well as all her help with data analysis and interpretation. I also thank Yamile Molina from the University of Washington for her tremendous assistance with methodology and the statistical analysis. Thank you to the Monteverde Cloud Forest Reserve (MVCFR) for allowing me access to reserve buildings to conduct my observations. Thank you to the CIEE Tropical Biology program for providing funding for supplies and giving me the opportunity to complete this project.

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