

A developmental test of the dominance-nutrition hypothesis: linking adult feeding, aggression, and reproductive potential in the paperwasp *Mischocyttarus mastigophorus*

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Received 14 November 2007, accepted 21 April 2008

Because adult females of primitively eusocial insects are plastic in their social roles, they are excellent models for assessing factors that affect fecundity and its relationship with dominance. Previous cross-sectional studies led to the dominance-nutrition hypothesis, which posits that the nutritional costs and benefits of task performance determine ovary development, and thereby affect female's dominance status. In this study, we investigate developmental predictions of the dominance-nutrition hypothesis in the paper wasp *Mischocyttarus mastigophorus*. Females were relatively inactive when young, and showed limited ovary development until over 2 weeks of adult age. As females aged, inter-individual variance in rates of behavior and in oocyte development increased significantly. As predicted by the dominance-nutrition model, females developed along diverging pathways, which were associated with worker-like and queen-like behavior and physiology. Individuals differed in their rates of nutritionally favorable (taking food from foragers) and nutritionally expensive (flying from the nest to forage) behavior. High rates of taking food from foragers were correlated with accelerated onset of giving social aggression (chases/bites) and with increased ovary development. Conversely, receiving aggression typically preceded the onset of foraging, and high rates of receiving aggression were positively associated with earlier onset of foraging. Our data do not support part of the dominance-nutrition model: ovary development did not precede the onset of elevated aggression. Variation in ovary development did not correlate positively with rates of giving aggression for young females. Our data implicate adult nutrition as an important factor for behavioral and physiological development, including the developmental onset of social aggression.

KEY WORDS: age polyethism, aggression, nutrition, social dominance, division of labor, development.

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INTRODUCTION

Social species often exhibit greater variability in female reproductive success than is predicted by sexual selection models, raising questions about the causes of variation in fecundity (HAUBER & LACEY 2005). In some species of social insects, individuals enter adulthood with few reproductive options (WHEELER 1986, GADAGKAR et al. 1988, O'DONNELL 1998a, FUKATSU et al. 2005, HARTFELDER et al. 2006). However, in social vertebrates and at least some primitively social insects, most if not all individuals retain some direct reproductive potential throughout their lifetime (LITTE 1979, SINHA et al. 1993, CLUTTON-BROCK et al. 2006, DESHPANDE et al. 2006). In these reproductively plastic species, adult experience may mediate reproductive status. Identification of behavioral and physiological correlates of fecundity is important to understanding the causes of reproductive division of labor in these species.

Independent-founding eusocial paper wasps (Vespidae Polistinae) such as *Mischocyttarus mastigophorus* are excellent taxa for analyzing the effects of physiological and behavioral factors on adult reproductive capacity. In some of these species, many or all adult females are capable of direct reproduction, but only socially dominant nest mates exhibit mature ovary development and oviposit (PARDI 1948, WEST-EBERHARD 1969, STRAMBI 1985, CHANDRASHEKARA & GADAGKAR 1992). Both social and reproductive dominance are often negatively associated with performing certain tasks, particularly foraging. Foraging is energetically costly for flying insects (O'DONNELL & JEANNE 1995, HARRISON & ROBERTS 2000), removes individuals from reproductive opportunities on the nest (REEVE 1991), and potentially exposes them to dangers such as predation (CLARK & DUKAS 1994).

The dynamics of female social status and fecundity (WEST EBERHARD 1981) are associated with variation in access to food (PARDI 1948, HUNT 1994). Correlational studies of adult behavior and physiology on *M. mastigophorus* suggested a series of directional connections between behavior and physiology, which were formalized as the dominance-nutrition hypothesis (MARKIEWICZ & O'DONNELL 2001). This model posits that nutritional profiles determine ovary development, and thereby affect social aggression and task performance. MARKIEWICZ & O'DONNELL (2001) based their conclusions on a cross-sectional

study. The goal of our study was to extend previous work by following individual female development. Longitudinal data may provide additional information about the directionality of the associations (i.e., temporal ordering of behavioral and physiological changes), and may support or refute causal relationships posited by the model. To the extent that age affects adult female physiology, age may also impact associations among reproductive potential, social dominance and task performance. In this study, we examine how relationships between task performance, social dominance, and reproductive potential develop in *M. mastigophorus* females. We focused on four key behavioral acts: leaving the nest to forage, taking food from foragers, and giving and receiving social aggression. We also measured ovary development as an indicator of reproductive potential. We analyzed relationships between behavior and physiology in three ways.

First, we examined the developmental ordering of behaviors and ovary development. The dominance-nutrition hypothesis posits that nutrient stores are a necessary precursor for ovary development. The model also posits that ovary development determines rates of giving aggression (PARDI 1948, WEST-EBERHARD 1969, RÖSELER 1991). This leads to the following developmental predictions: food-taking behavior should precede ovary development, and increases in ovary development should precede elevated social aggression. We predicted that individuals that took food from foragers more frequently would have enlarged oocytes and begin to give aggression to nestmates at earlier ages, and that they would delay or avoid foraging. Conversely, aggression from nest mates may modify nutritional and reproductive profiles, and accelerate the onset of, as well as increase the frequency of, foraging (SCHULZ et al. 2002, TOTH et al. 2005, TOTH & ROBINSON 2005, BRUYNDONCKX et al. 2006).

Second, we examined developmental changes in rates of these behaviors as well as changes in their associations with each other. We expected females' behavior to diverge as they aged. Rather than a predictable progression through a uniform series of social roles, we expected females to differentiate into queen-like and worker-like roles as they aged. Subordinate females should forage at increasing rates with age, while dominant females should not. Ovary development should also diverge with age: dominant females' oocytes should increase in size with age, while subordinate females' oocytes should not develop. We predicted similar correlations among behaviors on a daily basis, after accounting for age effects. For example, individuals' daily rates of taking food and giving aggression should be positively associated; daily rates of receiving aggression and foraging should also be positively associated.

Finally, we explore relationships among individuals' total frequency of performing key behaviors, summed across their adult lifespan, and their reproductive capacity. We used ovary development as an index of reproductive potential. We use these data to assess if associations among nutrition, behavior and reproductive potential are additive and cumulative. We predicted that individuals with a history of taking food and giving aggression would have "queen-like" reproductive physiology. Conversely, individuals who spent more time as foragers, and who received more aggression, should have less developed oocytes.

MATERIALS AND METHODS

Study site and subject colonies

Data were collected from 27 July to 7 September 2006 from five post-worker emergence *M. mastigophorus* colonies. The nests were observed in situ in Monteverde, Costa Rica (10°18'N, 84°49'W; O'DONNELL 1998b, MARKIEWICZ & O'DONNELL 2001). The observation nests were located on the eaves of buildings. We collected and individually marked all wasps on observation nests with paint pens 1-2 days before collecting behavioral data. We excluded these age-unknown wasps from analyses.

Only age-known females (N = 76) were included in analyses. We obtained most of the known-age subjects (N = 54, N = 9 to 14 per subject nest) as they emerged on their natal nests. The subject colonies were surveyed daily, and newly emerged females were captured, anesthetized with ether, marked with paint pens, and returned to their nests. To increase the sample size of known-age wasps, we also introduced adults (n = 22; n = 2 to 6 per subject nest) that emerged from other colonies. These additional females emerged from source combs that had been collected from nearby colonies. We maintained source combs in plastic containers in the laboratory. We marked females 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, S. O'DONNELL pers. obs).

Behavioral data collection

We observed each colony every 3 days, except that occasional observation days were skipped due to heavy rainfall. The order of observing colonies was not altered. For the first 2 days of each 3 day observation cycle, behavioral data were collected on two colonies per day (day 1: colonies A and B; day 2: colonies C and D). On the third day, behavioral data were collected on one colony (colony G). Behavioral data were collected continuously for 3 hr in the morning (1.5 hr per colony), between 07:00-10:00 hr local time, and for 2 hr in the afternoon (1 hr per colony), between 12:00-14:00 hr. We observed colonies on a total of 11 to 14 days over the course of 35 to 42 days.

We collected behavioral 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 behavioral acts were noted for all individuals present: arrivals and departures from the nest with time to the nearest minute, giving aggression (chasing and biting nest mates), receiving aggression, and taking food from incoming foragers (see ITÔ 1985 and O'DONNELL 1998b for descriptions of *Mischocyttarus* behavior). The study did not measure aggressive solicitation and its possible effects on the receipt of solids and liquids, and therefore cannot evaluate the possible contribution of that aspect of aggressive behavior as a possible cause of differential access of adults to nutrients (see Discussion). Aggressive solicitation could be the first step in differential access to nutrients, and to differences in ovarian development associated with further increases in social dominance. We used the timing of arrivals and departures to calculate time spent on the nest. Queens were identified based on observations of egg laying; one female per colony laid eggs during the study.

Collection of subjects and ovary dissections

Colonies were collected the evening of the last behavioral observation day. Ages of wasps collected at the end of the study (N = 60) ranged from 1 to 46 days. We stored

wasps individually in aldehyde-based fixative (Prefer fixative; Anatech, Ltd) for approximately one month before dissection (MOLINA & O'DONNELL 2007). The ovaries were removed from each female's gaster and photographed using a digital camera mounted on a dissecting microscope at a fixed magnification (10 ×). Length and width of the two largest oocytes from each female were measured from the digital photographs using Adobe Photoshop. Measurements were converted to millimeters, as calculated from digital images of a stage micrometer taken with the same equipment at the same magnification. Because oocytes are roughly elliptical, their area was calculated as: $\pi * \frac{1}{2} \text{ length} * \frac{1}{2} \text{ width}$. In multivariate analyses, we used the mean area of the two largest oocytes as an index of ovary development for each female (KEEPING 2000, 2002; MARKIEWICZ & O'DONNELL 2001; FOSTER et al. 2004). MARKIEWICZ & O'DONNELL (2001) showed that the mean length of eggs laid in *M. mastigophorus* nests was 1.1 mm. We used oocyte length to compare female's oocyte development to the size of mature eggs ($\geq 1.1\text{mm}$), and to identify females with partially-developed ovaries ($< 1.1\text{ mm}$). We also calculated mean oocyte length for the entire sample of females.

Statistical analyses

We accounted for colony identity in all analyses. Behavioral data that did not meet assumptions of parametric tests (e.g., unequal variances) were square-root transformed or non-parametric tests were used (e.g., Spearman's *r*, PEDHAUZER 1982). Unless explicitly stated, we performed within-subject analyses on behavioral data. We utilized between-subject tests when investigating individual and age-related variation in oocyte development.

Survival analysis

To describe developmental sequences of behaviors, we used the age (in days) at first observed performance for key behaviors (i.e. foraging for food, giving and receiving aggression, and taking food from foragers) as an indicator of onset of activity (O'DONNELL 2001, 2003; GIRAY et al. 2005). We analyzed the effects of covariates on the age of first performance of behaviors using the survival analysis nonparametric Wilcoxon test (SAS Institute SAS 9.1, 2006). Survival analysis provides unbiased estimates of time distribution parameters by including censored values (PYKE & THOMPSON 1986). Females that had not performed the response behavior before the study ended were entered into the survival analysis as censored values. We also used the Wilcoxon test to quantify differences in the age at first performance among all behaviors, and we then made pair wise comparisons among behaviors. We applied a Bonferroni correction for inflated type I error rates to these pair wise comparisons (critical *P*-value for significance was set at 0.0083).

We do not report data on pulp foraging and nest construction. As found previously (O'DONNELL 1998b), *M. mastigophorus* queens and the nest-highest ranking workers generally collected and used nest material for construction, and these acts were rarely performed by our known-age subjects (Y. MOLINA unpubl.).

Daily rates of behavior

For each wasp, we also calculated daily rates of behavior (frequency/hour spent on nest) for the following acts: giving aggression, receiving aggression, and taking food

from incoming foragers. We calculated daily foraging rate as the frequency of arrivals at the nest per observation hour. We used multiple regression analyses to analyze whether individuals differed in their mean daily rates of behavior, and whether daily rates of performance changed with age. We performed partial correlations among daily rates of behaviors, after accounting for individual and age effects. We calculated Levene's variance tests to examine age-related changes in behavioral and physiological variances. All individuals were included in these analyses, including those that disappeared before the end of the study.

Principal components analysis

We used principal components analysis to ascertain associations between all individuals' total frequencies of performing behavioral acts with their degree of ovary development. For this analysis, we quantified individuals' total frequency of performance for key behaviors over the course of the study, by estimating the total number of times each individual performed the behaviors during the study. To calculate the total frequency of performance, we summed all observed behavioral acts during the individual's lifespan. We adjusted these values to correct for unequal observation effort among individuals. We examined relationships among behavioral and physiological variables with the first two principal components, which explained the majority of observed variation in these variables. We assessed the strength of relationships among variables by noting which ones were significantly correlated (squared multiple correlations) with each principal component.

We identified the age at which fully-developed oocytes (1.1 mm long) first appeared, and then we used this age as a cutoff for analyzing early developmental patterns. We performed a second principal components analysis on the females younger than the age at which wasps with mature oocytes are first found, to ascertain associations between behavior and partial ovary development. As above, we assessed the strength of associations among variables by noting which ones were significantly correlated (squared multiple correlations) with the first two principal components.

RESULTS

Age at onset of behavior and ovary development

The colonies did not differ in the distribution of ages at first performance of giving and receiving aggression, taking food, and foraging (Survival analysis Wilcoxon test; all $df = 4$, all $\chi^2 < 2.75$, all $P > 0.60$). We pooled the colonies for the remainder of the analyses of age at first performance. Some individuals never performed certain behavioral acts before they were collected: 58% received aggression, 61% took food from foragers, 58% gave aggression and 53% foraged. Females that did not perform a given behavior were included, but censored, in survival analyses.

Wasps did not develop mature oocytes until at least 18 days of adult age. Thus, average age at onset for all behaviors preceded the development of layable eggs (Fig. 1). Females typically participated in aggressive interactions, and took food, before they began to forage (receiving aggression: Wilcoxon $\chi^2_1 = 45.9$, $P < 0.0001$; taking food: Wilcoxon $\chi^2_1 = 20.30$, $P < 0.0001$; giving aggression: Wilcoxon $\chi^2_1 = 12.10$, $P = 0.0005$; Fig. 1).

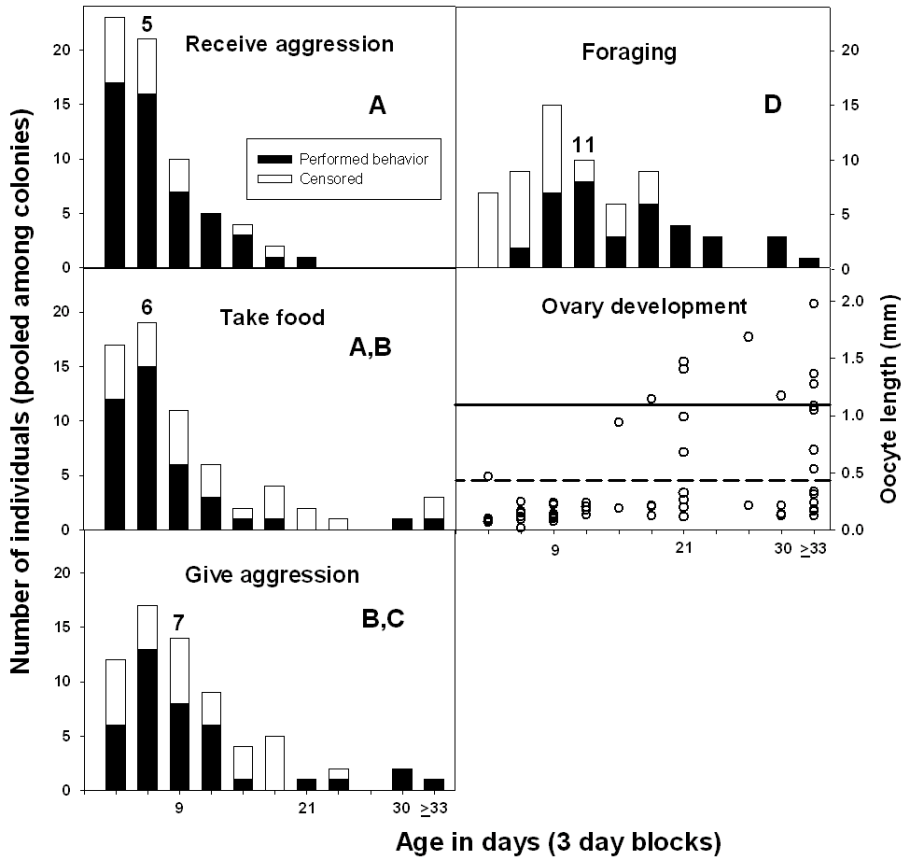


Fig. 1. — Bar graphs depict age of first performance (observed and censored values) of four behaviors for *M. mastigophorus* females from six colonies. Letters on each graph indicate significant differences in the distribution of age of first performance among behaviors (Survival analysis Wilcoxon tests with Bonferroni correction). Numbers above bars indicate median age (in days) at first performance for each behavior. The scatterplot depicts individual variation in oocyte length versus age. The solid horizontal line indicates the mean size of mature oocytes (1.1 mm); the dashed horizontal line indicates the average oocyte size for all females (0.42 mm).

Receiving aggression appeared to be particularly important to the onset of foraging. All foragers received aggression from nest mates. The majority of wasps that foraged first received aggression before (59%) or on the day of (20%) first foraging (Within-subjects Sign test, $M = 12.0$, $P < 0.0005$). Furthermore, wasps' daily rates of receiving aggression increased leading up to the onset of foraging ($F_{1,171} = 80.9$, $P < 0.0001$), and rose dramatically on the day of first foraging (Fig. 2). The amount of aggression an individual received also influenced age at onset of foraging: wasps that received aggression at higher daily rates began foraging at younger ages (between subjects, Wilcoxon $\chi^2_1 = 8.20$, $P = 0.004$).

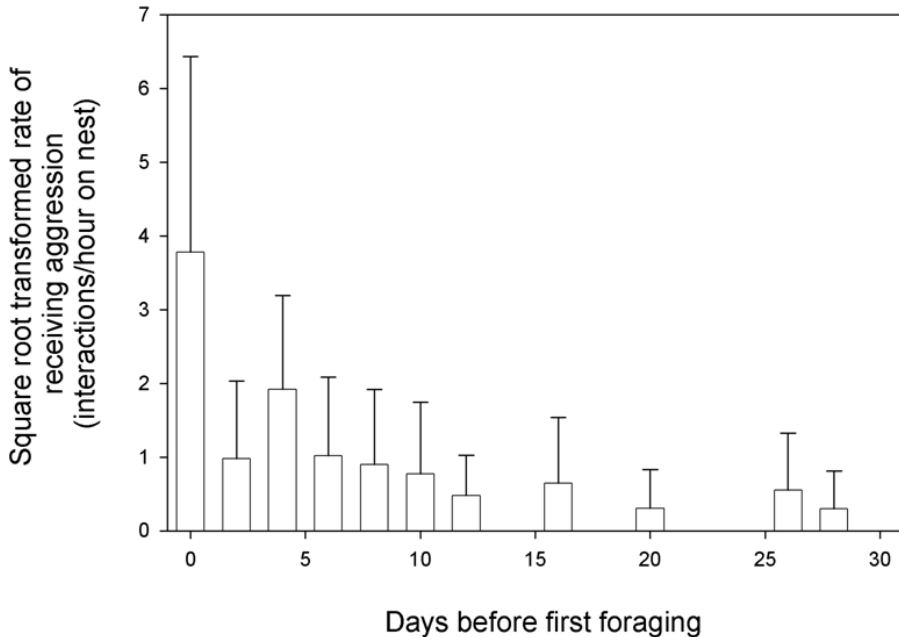


Fig. 2. — Bar graph depicting mean \pm SD rate of receiving aggression, looking back in development from the day of first foraging, for *M. mastigophorus* females from six colonies.

Ages of first performance did not differ significantly between taking food and receiving aggression (Wilcoxon $\chi^2_1 = 3.14$, $P = 0.08$). There were significant differences in the age at onset of giving and receiving social aggression: individuals received aggression significantly earlier than they gave aggression (Wilcoxon $\chi^2_1 = 12.40$, $P = 0.0004$). Age of performance did not differ between taking food and giving aggression (Wilcoxon $\chi^2_1 = 2.25$, $P = 0.13$), but daily rates of taking food from foragers influenced the onset of giving social aggression. Individuals that took food from foragers more frequently began to give aggression to nestmates at earlier ages (between subjects, Wilcoxon $\chi^2_1 = 4.16$, $P = 0.04$).

Developmental changes and divergence in rates of behavior and physiology

All wasps were relatively inactive early in adult life. As females aged, daily rates of giving and receiving aggression, and of foraging, increased (between subjects, Table 1). Daily rates of taking food did not change with age. Oocyte size was also positively correlated with age (between subjects, Spearman's $r = 0.66$, $P < 0.001$). However, the increases in behavioral rates and ovary development were not uniform among subjects. Variance in rates of all behaviors increased significantly with age, as did variance in oocyte size (between subjects, Table 2, Fig. 1). Wasps differed in daily rates of taking food, as well as in daily rates of giving aggression (between subjects, Table 2), but

Table 1.

Results of multiple linear regression analysis for identity, age and identity \times age interactions on daily rate of performance of four key behaviors in *M. mastigophorus* females. All behavioral rates were square-root transformed, and colony differences were accounted for in each analysis. Significant effects are indicated in bold.

Behavior	ID (t_{342})	Age (t_{342})
Foraging	- 0.95, $P = 0.34$	5.48, $P < 0.0001$
Take food	2.74, $P = 0.006$	- 0.94, $P = 0.35$
Direct aggression	2.21, $P = 0.03$	2.90, $P = 0.004$
Receive aggression	- 1.77, $P = 0.08$	2.86, $P = 0.004$

Table 2.

Results of Levene's variance tests on daily behavioral rates and ovary development. Significant results indicate age-related differences in variance.

	df	F	P
Oocyte Size	30,290	2.86	0.003
Foraging	42,360	2.31	0.0001
Take food	42,360	5.43	0.0001
Direct aggression	42,360	4.60	0.0001
Receive aggression	42,360	10.54	0.0001

individuals did not differ significantly in daily rates of foraging and receiving aggression. After controlling for age effects, daily foraging rates were positively correlated with rates of receiving aggression ($r = 0.38$, $df = 399$, $P < 0.0001$). Daily rates of taking food from foragers were positively associated with daily rates of giving aggression ($r = 0.17$, $df = 399$, $P = 0.001$).

Total behavioral experience and reproductive capacity

We analyzed the first two factors that resulted from a principal components analysis of total behavioral frequencies, age, and ovary development for all age-known wasps (between subjects, Table 3). The first PC factor accounted for 51% of the variance, and was correlated positively with age, foraging rate, and receiving aggression. Taking food and ovary development were positively correlated with the second PC factor, which accounted for an additional 17% of the variance. The second PC factor was negatively correlated with both receiving aggression and foraging.

Ovary development and behavior of young females

Oocyte size varied among young females, but most individuals (31/33) had poorly developed oocytes that were smaller than the average size (0.42

Table 3.

Results of Principal components analysis and squared multiple correlations (SMC) with variables ($df = 58$). Significant correlations are indicated in bold.

	PCI Factor loading	PCI SMC	PCII Factor loading	PCII SMC
Ovary Development	0.57	0.18, $P = 0.17$	0.51	0.51, $P < 0.0001$
Age	0.90	0.29, $P = 0.02$	0.03	0.03, $P = 0.82$
Foraging	0.88	0.29, $P = 0.02$	- 0.28	- 0.28, $P = 0.03$
Take food	0.46	0.15, $P = 0.25$	0.71	0.70, $P < 0.0001$
Give Aggression	0.51	0.16, $P = 0.11$	- 0.13	- 0.12, $P = 0.36$
Receive Aggression	0.85	0.27, $P = 0.04$	- 0.39	- 0.38, $P = 0.003$

mm) until at least 15 days after emergence (Fig. 1). We analyzed the first two factors from a principal components analysis of total behavioral frequencies, age, and ovary development for wasps aged 0-17 days post-emergence (between subjects, $n = 33$). The first PC factor accounted for 37% of the total variance, and was positively correlated with age ($r = 0.39$, $df = 31$, $P = 0.02$) and with taking food from foragers ($r = 0.36$, $df = 31$, $P = 0.04$). Young females varied most strongly in the frequency of taking food from foragers, which was positively associated with age. The second PC factor explained an additional 18% of total variance, and was negatively correlated with oocyte size ($r = - 0.58$, $df = 31$, $P = 0.0004$) and positively associated with both giving ($r = 0.36$, $df = 31$, $P = 0.04$) and receiving aggression ($r = 0.47$, $df = 31$, $P = 0.006$).

DISCUSSION

Behavioral links to reproductive physiology are well-established in reproductively plastic social species, especially in independent founding eusocial paper wasps (PARDI 1948, RÖSELER 1991, O'DONNELL 1998b). Hypothesized physiological mechanisms involved in reproductive division of labor among foundresses, and between castes, include changes in endocrine activity and the flow of nutrition (BOHM 1972, ROBINSON et al. 1992, MARKIEWICZ & O'DONNELL 2001, GIRAY et al. 2005, TOTH et al. 2005). PARDI (1948) and MARKIEWICZ & O'DONNELL (2001) presented data confirming associations among nutrient storage, ovary development and social aggression.

The dominance-nutritional model includes directional causal pathways linking each behavioral and physiological parameter. The model assumes that nutrient stores are a necessary precursor for ovary development. The fat bodies provide nutrients including necessary yolk precursor proteins for ovary development and hence, female's fat bodies must develop prior to mature oocytes (RAIKEHL & TARLOCHAN 1992, CANAVOSO et al. 2001, HAYS & RAIKHEL

2005). To the extent that taking food from foragers is needed to enhance fat body development, taking food should precede the onset of oocyte growth, particularly the appearance of mature oocytes. Nutrient stores should then bolster ovary development, which will in turn influence dominance behaviors such as giving aggression.

According to our results, *M. mastigophorus* females first proceed through an "idle" phase, in which all wasps are generally inactive. During this time, *M. mastigophorus* females have poorly developed ovaries and hence low reproductive capacity when young, for about 2 weeks after adult emergence. Individual variation in behaviors related to fat body development preceded the development of mature oocytes. Indeed, the strongest difference among young females was frequency of taking food from foragers. This may have been correlated with degree of aggressive solicitation, a common correlate and indicator of social dominance (PARDI 1948, WEST-EBERHARD 1969, HUNT 1994) which we did not measure (Methods). Strong individual variation in acquiring nutrients (taking food) was not linked to ovarian condition in young females, but taking food was positively correlated with ovary development when including all females in the analysis. Ovary development increased with age for a subset of females. Taking food may have influenced the likelihood of developing mature oocytes. Our findings show that individual variation in taking food occurs prior to the capacity to develop mature oocytes, and may thereafter exaggerate the developmental bifurcation of worker-like and queen-like physiological profiles.

We found positive associations of ovary development and social aggression. However, contrary to the dominance-nutrition model's second prediction, our results suggest that young females with larger oocytes engage less frequently in social aggression. Furthermore, the developmental onset of giving aggression preceded the age of increasing ovary development. Nutritional stores may mediate the developmental dynamics of queen-like behavior and physiology. Females may only begin to give aggression once they have adequately sized fat bodies. In support of a link between nutrition and dominance, females that took food at high rates began to dominate nest mates at younger ages. Furthermore, wasps' daily rates of taking food and dominating nest mates positively correlated.

Our data suggest that receiving aggression induces foraging. Individuals that did not receive aggression also did not forage, and receiving aggression usually developmentally preceded or coincided with the start of foraging. Higher rates of receiving aggression were strongly related to lower age at onset of foraging, and foraging rates were positively correlated with rates of receiving aggression.

In many highly eusocial species, offspring workers undergo a stereotyped behavioral sequence known as temporal polyethism. Workers generally begin with in-nest tasks (e.g., nest maintenance) and culminate with off-nest tasks (e.g., foraging) (JEANNE 1991, ROBINSON et al. 1992 but see SEID & TRANIELLO 2006). Individual workers can differ in the rate of behavioral development, but they pass through a predictable sequence of tasks (JEANNE 1991). Temporal polyethism is best-documented in species with strong caste differences, but evidence for temporal polyethism was recently presented for some independent-founded wasps (JEANNE 1991, GADAGKAR 2001, GIRAY et al. 2005). Our study does

not support the existence of temporal polyethism in *M. mastigophorus*. Not all individuals performed this study's key behaviors, nor did individuals perform all behaviors in the same order. Individuals also did not cease on-nest tasks after the onset of foraging for food, as is often found in advanced species (JEANNE 1991, ROBINSON et al. 1992, but see SEID & TRANIELLO 2006). Instead, variation in behavior and physiology increased between subjects as wasps aged.

The dominance-nutrition model effectively addresses changes in dominance status, but the model does not account for a developmental starting point. When in development do differences in dominance status begin, and how are they initiated? Our developmental data suggest that the establishment of divergent behavioral trajectories begins early in adult female development, and persists throughout the first several weeks of adult life. We found significant individual differences in rates of taking food in young females. Individual variation in nutrient stores may have then influenced increasingly disparate behavioral and physiological pathways. Total frequency of taking food positively correlated with the development of mature oocytes, suggesting cumulative effects of maintaining nutrient stores on reproductive physiology. Daily rates of taking food also positively correlated with daily rates giving social aggression, which differed significantly between individuals.

Variation in ovary development was low for young females, and we did not find strong relationships between oocyte variation and behavior early in life. Earlier studies showed that body size variation does not predict dominance or reproductive status in *M. mastigophorus* (MARKIEWICZ & O'DONNELL 2001). These patterns do not indicate strong pre-adult effects on caste differentiation. However, our study does not rule out the possibility of pre-imaginal biases in caste development that could be reflected in other physiological variables. Larval differences could bias the likelihood of individuals following worker-like or queen-like trajectories, although evidence of nutritional differences in *Mischocyttarus* larvae has been mixed (MURAKAMI & SHIMA 2006). Because all of our data were collected in the early wet season in Monteverde, we could not assess seasonal effects on caste determination (O'DONNELL 1996). Whether caste determination patterns might vary with season (particularly rainfall) for tropical independent-founding wasps is unknown, but *M. mastigophorus* colonies are founded, and males are present, throughout the year in Monteverde. These patterns suggest that adult females have opportunities to initiate new nests throughout the year, and that potential queens are produced year-round (O'DONNELL & JOYCE 2001; S. O'DONNELL pers. obs). Further study is needed to differentiate between larval and adult nutrition and experience on worker-like versus queen-like behavior and physiology. Regardless of possible pre-imaginal biases, however, our study demonstrates the importance of social interactions and adult nutrition to the development of behavioral dominance and task performance.

ACKNOWLEDGEMENTS

Thanks to Mary Jane West-Eberhard, Anjali Kumar, and several anonymous reviewers for helpful comments on earlier drafts of the manuscript. Research was conducted

under permits from the Ministry of the Environment and Energy, Republic of Costa Rica, Scientific Passport #0387, and in accordance with the laws of the Republic of Costa Rica. The research presented was supported by the National Science Foundation, while S. O'Donnell was working at the foundation. Any opinions, findings, and the conclusions or recommendations, are those of the authors, and do not necessarily reflect the views of the National Science Foundation. Thanks to the Organization for Tropical Studies for ongoing research support, including assistance in obtaining permits. Funding was provided by NSF grant NSF-IBN 0347315 to S. O'Donnell (Replacement PI Eliot Brenowitz).

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