

Daniel A. Markiewicz · Sean O'Donnell

Social dominance, task performance and nutrition: implications for reproduction in eusocial wasps

Accepted: 18 April 2001 / Published online: 22 June 2001
© Springer-Verlag 2001

Abstract Dominance status is associated with individual differences in reproductive capacity in many animal societies, but the mechanisms that link social dominance to reproductive physiology are poorly understood. We propose a model for social dynamics that incorporates the nutritional costs and benefits of behavior: dominant individuals avoid energy-expensive behavior and build their nutritional reserves, thereby increasing their potential for reproduction. Greater reproductive capacity, once achieved, favors increased social dominance. To test the model, we measured relationships of females' nutrient storage and reproductive capacities with dominance status and task performance in the eusocial wasp *Mischocyttarus mastigophorus*. Ovary development was positively related with high levels of nutrient storage and with high rates of dominance behavior, but was not correlated with task performance. In contrast, high levels of nutrient storage were positively related with the performance of nutrient garnering and conserving tasks, but not with dominance behavior. These data support a model which places the nutritional costs of task performance as an intermediate causal link that connects dominance status with the accumulation of nutrient stores. Nutrient flow may be a general causal mechanism linking dominance status to reproductive capacity in animal societies.

Keywords Caste · Fat body · Ovary development · Polyethism · Vespidae: *Mischocyttarus*

Introduction

Social status corresponds with variation in reproductive physiology for many group-living animals. Reproduc-

tively potent individuals typically dominate their group mates, and dominance status, in turn, affects division of labor within groups. Dominant individuals often avoid performing risky or energy-expensive behavior (cooperatively breeding birds: Brown et al. 1997; primates: Lazaro-Perea et al. 2000; naked mole rats: Jacobs and Jarvis 1996; African wild dogs: Creel et al. 1997; eusocial insects: West-Eberhard 1981). The dynamics of animals' social status may result from an interaction of behavior and physiology. However, the physiological mechanisms that connect changes in social status with variation in reproductive physiology are not well understood. We propose a directional feedback model that links dominance status with reproductive physiology, through the nutritional effects of task performance on animals' energy balance. We present a test of this model on the eusocial paper wasp *Mischocyttarus mastigophorus*, and suggest additional comparative and experimental tests of the model.

Independent-founding eusocial wasps (paper wasps, Vespidae) have been important subjects for analyzing the relationships of social behavior with physiology. Dominance hierarchies form both in newly-initiated paper wasp colonies (cofoundress associations), and on post-emergence nests that have produced female offspring. Female paper wasps' dominance status often depends strongly on their reproductive physiology (Pardi 1948; Röseler et al. 1985). The queen is the female with the highest degree of ovary development. The queen typically dominates all other females, and she largely monopolizes reproduction while avoiding costly tasks such as foraging (Strassmann and Meyer 1983; O'Donnell 1998a, 1998b). Dominance interactions can also occur between offspring workers, and workers' dominance status affects their task performance (Pardi 1948; Jeanne 1972; Litte 1977, 1981; Chandrashekara and Gadagkar 1991; O'Donnell 1998a). Cofoundress and offspring female paper wasps exhibit considerable behavioral and physiological plasticity. Differences in ovary size increase after a dominance hierarchy is established (West-Eberhard 1969; Röseler et al. 1980,

D.A. Markiewicz (✉) · S. O'Donnell
Department of Psychology, University of Washington,
Box 351525, Seattle, Washington 98195, USA
E-mail: dmarkie@u.washington.edu
Tel.: +1-206-5432315
Fax: +1-206-6853157

1984; Dropkin and Gamboa 1981). Furthermore, the most dominant cofoundresses or offspring workers are likely to ascend to the reproductive position following changes in social structure, such as death of the queen (O'Donnell 1996; but see Sinha et al. 1993).

West-Eberhard (1981; see also Jeanne 1991) hypothesized that division of labor in insect colonies results from variation in females' physiological capacities to produce offspring. West-Eberhard predicted that reduced capacity to reproduce would result from performance of worker-like tasks such as foraging. Conversely, the females that specialize on queen-like tasks associated with egg laying and offspring care would enjoy increased fecundity. However, the causal relationships linking division of labor with reproductive physiology have not been identified. It is not known whether females' reproductive capacities cause or result from variation in dominance status (Röseler 1991). Hunt (1991) suggested that energy balance could be a general mechanism that connects variation in dominance status with reproductive capacity. Dominant female paper wasps are more likely to take food loads from foragers, and less likely to pass food to adult nestmates (Pardi 1948; Jeanne 1972; O'Donnell 1995, 1998a). In *M. mastigophorus*, as in other *Mischocyttarus* species, dominant individuals also foraged at lower rates (Jeanne 1972; Litte 1977; O'Donnell 1998a). By avoiding the energetic costs of foraging, dominant individuals may augment the trophic advantage they gain from unequal exchanges of food.

In this paper we extend West-Eberhard's (1981) model of social dynamics by incorporating the nutritional effects of queen-like and worker-like behavioral roles on reproductive physiology. In our model, we assume that variation in nutrition affects females' reproductive capacities, and that sufficient energy stores are a physiological prerequisite for reproduction (Wheeler 1994; Wheeler and Martinez 1995). We also assume that queen-like behavior is more energetically favorable to females than worker-like behavior (O'Donnell and Jeanne 1995a, 1995b). We predict that by avoiding costly tasks, dominant females will have a positive energy balance and accumulate greater nutrient stores. Greater nutrient stores will increase females' potential for direct reproduction. Increased reproductive development, in turn, will promote elevated dominance status. The converse relationships should also hold. We predict that subordinate females will perform tasks that deplete their energy stores, thereby reducing their capacity for direct reproduction. Decreases in fecundity should cause lower dominance rankings for the subordinate females.

To test our model, we measured individual variation in reproductive capacity, nutritional status, and behavior in post-emergence *M. mastigophorus* colonies. We used the size of the abdominal fat body, an organ used for lipid and protein storage and for production of egg yolk proteins, as an index of nutritional state (Kilby 1963; Keeley 1985; Wheeler 1994; Wheeler and Martinez 1995). We used ovary development as a measure of relative reproductive potential, and measured the rela-

tionships of the physiological variables with variation in dominance behavior and task performance.

We found that dominance had strong effects on task performance, with dominant females avoiding costly tasks (foraging) and consuming much of the food brought to the colony. Females' dominance status was more closely associated with ovary development than with fat body size. In contrast, fat body variation was most strongly associated with differences in food consumption and energy expenditure. Our results were consistent with the hypothesis that social dominance affects ovary development primarily through its influence on division of labor and nutrition.

Materials and methods

Behavioral observations and variables

We observed six *M. mastigophorus* colonies with adult offspring (post-emergence colonies) at Monteverde, Costa Rica (10° 18' N, 84° 49' W). Data on division of labor in these colonies were published previously (O'Donnell 1998a, 1999). We individually marked all adults on the nests with paint pens. Behavioral observations were conducted between 25 July and 11 August 1997. We collected behavioral data for three continuous hours in the morning (between 0800 hours and 1140 hours local time) and 2 continuous hours in the afternoon (between 1300 hours and 1630 hours local time) on 2 consecutive days per nest, for a total of 10 h observation time per colony (9 h total at one colony). We noted all occurrences of nest maintenance tasks, social interactions including dominance and submission, flying departures and arrivals, and transfers of food and building materials collected by the foragers (see O'Donnell 1998a for more details on behavioral data collection). A single female dominated all others and was identified as the queen in each colony; all other females are referred to as workers.

We calculated rates of dominance (total aggressive and subordinate interactions per hour on the nest) for each individual. Foraging rates were measured as the number of times an individual returned to the nest with prey or nectar per hour of observation. Rates of taking food were measured as the proportion of food forager arrivals during which a given female took food, including only those forager arrivals which occurred while that female was present on the nest.

Physiological measurements

On the evening of the second day of behavioral observations, we collected the colonies. We preserved adult wasps and their nests in Kahle's solution (18 parts 70% ethanol: 1 part glacial acetic acid: 1 part formalin). Wasps were stored in Kahle's solution for > 1 year, then transferred to 70% ethanol prior to dissection. We dissected the gasters (expanded portion of the abdomen) of the marked females for which behavioral data had been collected. Physiological measurements were performed blind to the behavior of the wasps being dissected. For each female we measured ovary development, inspected the condition of the fat body, and measured the length of the anterior (costa) vein of each wing as an indicator of body size. The amount of fat body present on the interior of the gastral tergites and sternites was scored as 0 (little or no fat body) or 1 (a thick layer of fat body tissue lining the body cavity).

Following fat body scoring, we dissected the viscera out of the gaster. The ovaries were dissected from the rest of the viscera and photographed at 20× magnification. We produced contact print sheets from the negatives and scanned the prints into computer files at 400 dpi resolution. Adobe Photoshop software was used to

digitize the photographs, magnify the images, and measure the oocytes. We determined an index of ovary development for each female by measuring the length of the largest oocyte in each ovary, and taking the mean of the lengths of these two oocytes. The measurements were calibrated to length in mm by photographing a 1-mm microscope stage micrometer at 20× magnification and measuring the image as above. We collected a sample of 14 eggs laid in the nest cells of three subject colonies to determine the size of mature oocytes. We measured the lengths of the laid eggs to the nearest 0.04 mm at 20× magnification with an ocular micrometer.

We dissected the forewings from the body of each wasp and mounted them on microscope slides with transparent tape. We scanned the wings into computer files at 300 dpi resolution, then measured them using the ruler tool of Adobe Photoshop software. For each wing we measured the length of the rigid anterior vein (the costa vein) from its proximal end to its distal end at the pterostigma. We took the mean of left and right wing measurements as an indicator of body size for each female.

Statistical analyses

We used multiple linear regression to analyze relationships between pairs of continuous variables, except when higher order regression models (exponential relationships) led to a significant improvement in the fit of the regression line. We included colony identity as a covariate in all regression analyses, and we nested other predictor variables within colonies. For multiple regression analyses where we tested the effects of multiple physiological or behavioral variables, we present the results for each variable when it was entered last in the regression model, i.e., after accounting for the effects of the other variables (Sokal and Rohlf 1981). We tested for effects of possession of mature oocytes by separating females into two classes: those with oocytes at or above the average size of laid eggs, and those with smaller oocytes. For these tests we corrected for colony effects using linear regression, then compared the ovary size classes using modified t-tests that did not assume equality of variance. Errors around means are ± 1 standard deviation (SD).

Results

We collected 57 marked females from the six subject colonies; the sample included 5 queens and 52 workers (the queen of one of the colonies was absent upon collection). Wasps with large fat bodies had significantly larger oocytes (Fig. 1, ANOVA, $F_{1,57}=9.01$, $P<0.05$). Because the two physiological measures were positively correlated, we estimated their independent relationships with behavioral variables using multiple linear regression. Wing length did not correlate significantly with any physiological or behavioral variable (all $P>0.05$), and will not be considered further.

Physiological correlates of dominance behavior

Females' rates of dominating nest mates increased exponentially with ovary development (inclusion of the quadratic term significantly improved the fit of the regression model; Fig. 2a, stepwise linear regression, $F_{1,57}=9.479$, $P<0.01$). Rate of dominance over nest-mates did not correspond with fat body condition (Fig. 2a, stepwise linear regression, $F_{1,57}=1.35$, NS). Workers with more developed ovaries were dominated by queens at higher rates (Fig. 2b, linear regression,

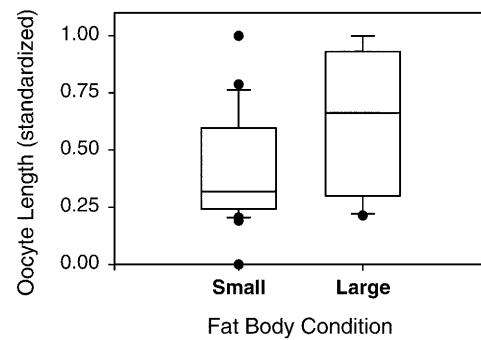


Fig. 1 Variation in the mean length of the two largest oocytes of *Mischocyttarus mastigophorus* females plotted against categories of fat body development. Mean oocyte lengths have been standardized by expressing values for all wasps of the same colony as fractions of the largest value observed in the colony. Box plots show medians, interquartiles, and 10% and 90% percentiles. Points represent more extreme values

$F_{1,52}=2.73$, $P<0.05$). Ovary development was not linearly related to domination by workers (linear regression, $F_{1,57}=1.83$, $P>0.10$), but females with mature oocytes (length >1.1 mm, which was the mean length of $n=14$ mature eggs collected from nests) were dominated by workers at lower rates (Fig. 2c, t -test, $t=2.803$, $df=37$, $P<0.01$). Ovary development was not correlated with domination by males (linear regression, $F_{1,57}=0.40$, NS), and workers and queens experienced similar levels of domination by males (t -test, $t=-0.019$, $df=48$, NS).

Females that were dominated at higher rates by workers also foraged at higher rates (stepwise linear regression, $F_{1,64}=8.09$, $P<0.01$), and females' foraging rates also correlated with rates of submission to males (stepwise linear regression, $F_{1,64}=7.98$, $P<0.01$). Foraging rate was not correlated with rate of domination by the queen (stepwise linear regression, $F_{1,64}=0.15$, NS). Workers that were dominated at higher rates by other workers had smaller fat bodies (Fig. 2c, ANOVA, $F_{1,52}=12.28$, $P<0.01$), and females that were dominated at higher rates by males showed a non-significant trend toward having smaller fat bodies (ANOVA, $F_{1,57}=4.69$, $0.05<P<0.10$). Workers' fat body development was not related to domination by the queen (Fig. 2b, ANOVA, $F_{1,52}=0.04$, NS).

Physiological correlates of foraging and food taking

Females' fat body condition correlated negatively with foraging rate (Fig. 3a, stepwise linear regression, $F_{1,57}=5.69$, $P<0.05$), and fat body condition correlated positively with the portion of observation time that wasps spent on the nest (Fig. 3b, stepwise linear regression, $F_{1,57}=21.48$, $P<0.001$). Oocyte length did not covary linearly with time on nest (Fig. 3b, stepwise linear regression, $F_{1,57}=0.00$, NS) nor with foraging rate (Fig. 3a, stepwise linear regression, $F_{1,57}=0.47$, NS). However, a threshold effect was apparent for females with mature oocytes: these females consistently foraged at low rates (t -test, $t=3.308$, $df=49.8$, $P<0.01$) and

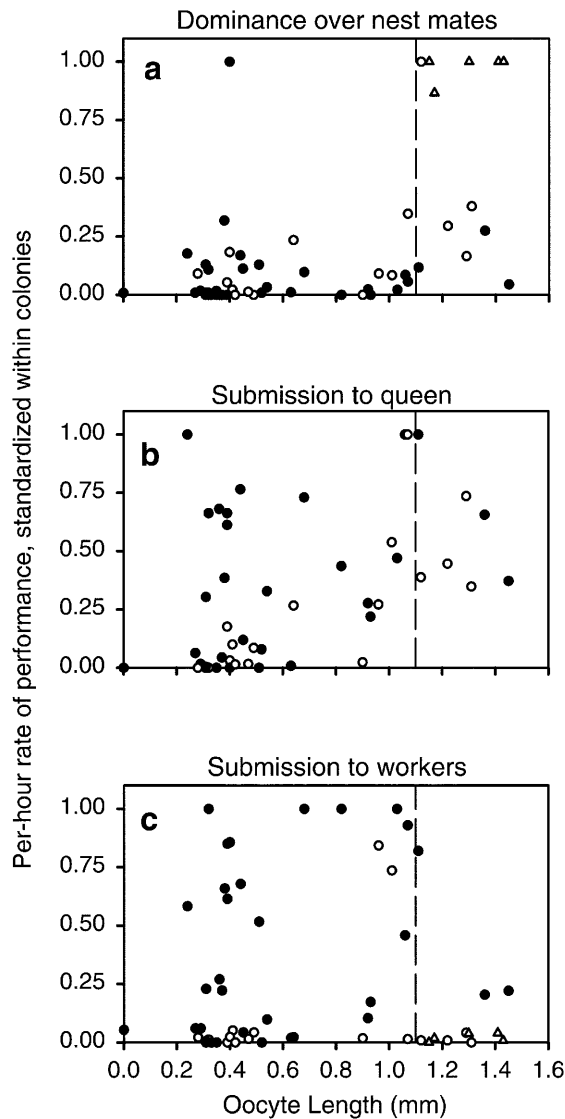


Fig. 2 Rates of dominance interactions (a dominance over nest mates; b submission to queen; c submission to workers) of female *Mischocyttarus mastigophorus* plotted against degree of ovary development and fat body condition. For clarity of presentation, rates of behavior were standardized among colonies by dividing by the maximum value within each colony. Workers are represented by circles, queens by triangles. Filled data points represent individuals with small fat bodies (score=0); open data points represent individuals with large fat bodies (score=1). The dashed line indicates an oocyte length of 1.1 mm

spent more time on the nest (t -test, $t = -3.561$, $df = 16.229$, $P < 0.01$; Fig. 3a, b). Rates of taking food from foragers correlated positively with both oocyte length (Fig. 3c, stepwise linear regression, $F_{1,57} = 18.41$, $P < 0.001$) and fat body condition (Fig. 3c, stepwise linear regression, $F_{1,57} = 6.02$, $P < 0.05$).

Discussion

Previous empirical research on paper wasp behavioral physiology has been largely restricted to cofoundress

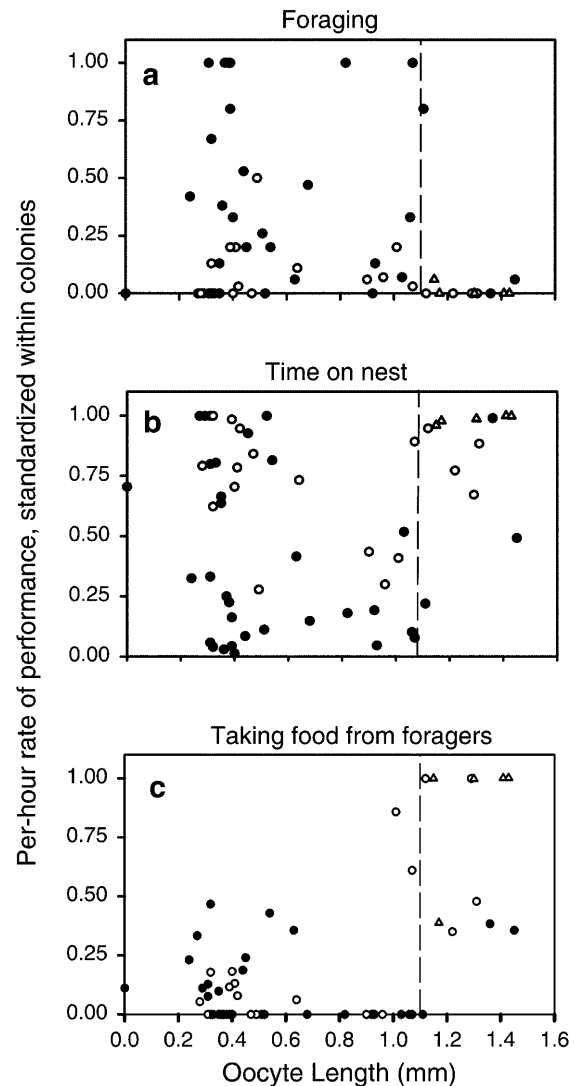


Fig. 3 Rates of foraging (a), amount of time spent on the nest (b), and food taking (c) for female *Mischocyttarus mastigophorus* plotted against degree of ovary development and fat body condition. See Fig. 2 legend for an explanation of the standardization of behavioral measures across colonies and the symbols used

associations in temperate wasp populations (Pardi 1948; Dropkin and Gamboa 1981; Röseler et al. 1985; Röseler 1991). Temperate paper wasps exhibit physiological adaptations for the overwintering of female reproductives (gynes), often including body size differences between gynes and workers (Eickwort 1969; West-Eberhard 1969; Haggard and Gamboa 1980; O'Donnell 1998c). The reproductive physiology of gynes is qualitatively different from that of offspring workers in temperate paper wasps. In contrast, many tropical habitats are relatively aseasonal, and paper wasp females initiate colonies during most months of the year (Jeanne 1972; Litte 1979, 1981; O'Donnell and Joyce 2001). In tropical paper wasps, offspring workers as well as cofoundresses are potential reproductives. Offspring are likely to supersede their mothers and become queens on

long-lived nests (West-Eberhard 1969; Jeanne 1972; Litte 1981). Tropical wasp females' reproductive physiology is relatively flexible, changing in response to social conditions and task performance. We found that body size variation was not associated with reproductive physiology or behavior in *M. mastigophorus* females, and that variation in female behavior and reproductive physiology were continuous.

Rates of dominating nestmates are correlated with ovary development in many species of independent-founding eusocial wasps (Dropkin and Gamboa 1981; Röseler et al. 1985; Turillazzi and Turillazzi 1985). Our results were consistent with these findings. However, workers' rates of submission to queens were related to ovary development, while their rates of submission to males and to other workers were not. These differences suggest that queen dominance functioned in direct reproductive suppression, while worker and male dominance did not. Instead, worker and male aggression were probably associated with competition over food resources (O'Donnell 1998a). Dominance interactions among workers, and between males and workers, may regulate polyethism and nutrient flow in *M. mastigophorus* colonies. High rates of subordination to workers and to males were correlated with high foraging rates (high energy cost) and low rates of taking food from foragers (low energy gain; O'Donnell 1998a, 1999). Furthermore, subordination to workers and males was correlated with smaller fat body sizes.

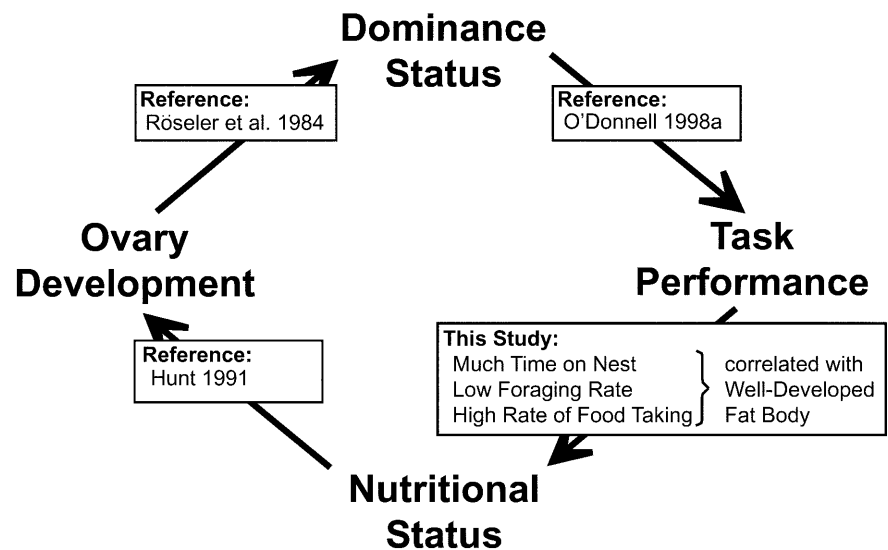
We hypothesize that dominance, task performance, nutrition and reproductive physiology form a feedback loop that determines social caste. The directional, causal links in our model (Fig. 4) are derived from the relative strengths of associations of behavior and physiology that we measured, and on relationships that have been documented in other eusocial paper wasps. We posit that energy balance underlies the dynamic system of caste determination of tropical paper wasps.

Previous work showed that *M. mastigophorus* females' task performance was strongly dependent on their dominance status (O'Donnell 1998a, 1999). Our data suggest that variation in fat body development was more closely associated with task performance differences, and presumably with their energetic consequences, than with dominance status. This pattern suggests that variation in nutritional physiology was determined principally by task performance differences. Experimental manipulations are needed to test this causal connection more directly. Because the fat body produces egg proteins, a well-developed fat body is a physiological precursor of oocyte development in female insects (Keeley 1985; Wheeler 1994). Ovary development, in turn, has been shown to influence females' dominance status (Röseler 1991). In our model, changes in females' behavioral and physiological status can be either positive or negative. For example, changes in colony composition can either increase or decrease an individual's relative dominance status. Therefore, our model accounts for the dynamic nature of females' positions in their colony's social structure (Jeanne 1972; West-Eberhard 1981; Jeanne 1991), and the model makes specific predictions about the mechanisms underlying these changes. Similar feedback systems that integrate dominance, energy balance, and reproductive physiology may be important in regulating the social structure of many group-living animals.

Larva-adult food exchange (trophallaxis) is a pathway of nutrient exchange not considered in our behavioral data set. Larval saliva can be a significant source of nutrients for adult female wasps (Ishay and Ikan 1968; Hunt et al. 1982). In systems where larva-adult trophallaxis is an important nutrient exchange pathway, our model predicts that females procuring a large share of the colony's supply of larval saliva will tend to rise in relative dominance rank and reproductive capacity.

Dominant individuals have better-developed ovaries in many species of eusocial paper wasps. However, the

Fig. 4 Flow model of hypothesized relationships between behavior, nutrition, and reproductive physiology in eusocial paper wasps



relationship between workers' dominance status and task performance varies among species (O'Donnell 1996). Reduced foraging by dominant individuals was found in several species of *Mischocyttarus*, including *M. mastigophorus* (Jeanne 1972; Litte 1977, 1981; O'Donnell 1998a). In contrast, dominant workers foraged more than their nestmates several species of *Polistes* (Strassmann and Meyer 1983; Miyano 1986; Hughes et al. 1987). In some species, the most active foragers possessed the most developed ovaries, and these foragers were also most likely to replace their queen if she died or was removed (Strassmann and Meyer 1983; Hughes et al. 1987; Hughes and Strassmann 1988). Foraging rates were not related to dominance or to reproductive physiology in *Ropalidia marginata* (Chandrashekara and Gadagkar 1992) or *P. biglumus* (Makino and Aoki 1982).

Predictions from our model (Fig. 4) about the allocation of food energy in the colony, and its effects on reproductive physiology, are difficult to make when dominant individuals forage. Foragers are likely to experience high energetic costs. However, the net energetic flow to an individual may also depend heavily on the amounts of food foragers consume themselves, and on how much they give up to adult nestmates. Comparative tests of our model should be directed at the independent-founding paper wasp species with dominant foragers. These studies should combine measures of reproductive physiology, dominance, foraging and food exchange. Experimental studies employing manipulations of colony energy balance (Rossi and Hunt 1988), social structure (Strassmann and Meyer 1983), and females' reproductive potential (Röseler et al. 1984) are also needed to further test our behavioral/physiological model.

Acknowledgements Sara Ranger and Nicolas Spang assisted with field research and behavioral data collection. Thanks to Frank Joyce, Alan and Marlene Pounds, the Monteverde Cloud Forest Reserve, and the Monteverde community for logistical support and access to private property for field research. The University of Washington Animal Behavior Group made helpful comments on the manuscript. We also thank two anonymous reviewers for their comments. Financial support was provided by grants to S. O'D. from the University of Washington Royalty Research Fund and the US National Science Foundation (IBN-9904885). Research permits were obtained from the Costa Rican Ministry of Natural Resources with the help of the Organization for Tropical Studies. The research complied with the "Principles of animal care", publication No. 86-23, revised 1985 of the National Institute of Health, and with the current laws of the Republic of Costa Rica and the United States of America.

References

Brown JL, Brown ER, Sedransk J, Ritter S (1997) Dominance, age, and reproductive success in a complex society: a long-term study of the Mexican jay. *Auk* 114:279–286

Chandrashekara K, Gadagkar R (1991) Behavioural castes, dominance, and division of labor in a primitively eusocial wasp. *Ethology* 87:269–283

Chandrashekara K, Gadagkar R (1992) Queen succession in the primitively eusocial wasp *Ropalidia marginata* (Lep.) (Hymenoptera: Vespidae). *J Insect Behav* 5:193–209

Creel S, Creel NM, Mills MGL, Monfort SL (1997) Rank and reproduction in cooperatively breeding African wild dogs: behavioral and endocrine correlates. *Behav Ecol* 8:298–306

Dropkin JA, Gamboa GJ (1981) Physical comparisons of foundresses of the paper wasp, *Polistes metricus* (Hymenoptera: Vespidae). *Can Entomol* 113:457–461

Eickwort K (1969) Separation of the castes of *Polistes exclamans* and notes on its biology (Hym.: Vespidae). *Insectes Soc* 16: 67–72

Haggard CM, Gamboa GJ (1980) Seasonal variation in body size and reproductive condition of a paper wasp, *Polistes metricus* (Hymenoptera: Vespidae). *Can Entomol* 112:239–248

Hughes CR, Strassmann JE (1988) Age is more important than size in determining dominance among workers in the primitively eusocial wasp, *Polistes instabilis*. *Behaviour* 107:1–15

Hughes CR, Beck MO, Strassmann JE (1987) Queen succession in the social wasp, *Polistes annularis*. *Ethology* 76:124–132

Hunt JH (1991) Nourishment and the evolution of the eusocial Vespidae. In: Ross KG, Matthews RW (eds) *The social biology of wasps*. Cornell University Press, Ithaca, pp 426–450

Hunt JH, Baker I, Baker HG (1982) Similarity of amino acids in nectar and larval saliva: the nutritional basis for trophallaxis in social wasps. *Evolution* 36:1318–1322

Ishay J, Ikan R (1968) Food exchange between adults and larvae in *Vespa orientalis* F. *Anim Behav* 16:298–303

Jacobs DS, Jarvis JUM (1996) No evidence for the work-conflict hypothesis in the eusocial naked mole-rat (*Heterocephalus glaber*). *Behav Ecol Sociobiol* 39:401–409

Jeanne RL (1972) Social biology of the neotropical wasp *Mischocyttarus drewseni*. *Bull Mus Comp Zool* 144:63–150

Jeanne RL (1991) Polyethism. In: Ross KG, Matthews RW (eds) *The social biology of wasps*. Cornell University Press, Ithaca, pp 389–425

Keeley LL (1985) Physiology and biochemistry of the fat body. In: Kerkut GA, Gilbert LI (eds) *Comprehensive insect physiology, biochemistry and pharmacology*, vol 3. Pergamon Press, Oxford, pp 211–248

Kilby BA (1963) The biochemistry of the insect fat body. *Adv Insect Physiol* 1:111–174

Lazaro-Perea C, Castro CSS, Harrison R, Araujo A, Arruda MF, Snowdon CT (2000) Behavioral and demographic changes following the loss of the breeding female in cooperatively breeding marmosets. *Behav Ecol Sociobiol* 48:137–146

Litte M (1977) Behavioral ecology of the social wasp, *Mischocyttarus mexicanus*. *Behav Ecol Sociobiol* 2:229–246

Litte M (1979) *Mischocyttarus flavitarsus* in Arizona: social and nesting biology of a polistine wasp. *Z Tierpsychol* 50:282–312

Litte M (1981) Social biology of the polistine wasp *Mischocyttarus labiatus*: survival in a Colombian rain forest. *Smithsonian Contrib Zool* 327:1–27

Makino S, Aoki S (1982) Observations on two polygynic colonies of *Polistes biglumus* in Hokkaido, Northern Japan (Hymenoptera, Vespidae). *Kontyû* 50:175–182

Miyano S (1986) Colony development, worker behavior, and male production in orphan colonies of a Japanese paper wasp, *Polistes chinensis antennalis* Perez (Hymenoptera: Vespidae). *Res Popul Ecol* 28:347–361

O'Donnell S (1995) Division of labor in post-emergence colonies of the primitively eusocial wasp *Polistes instabilis* de Saussure (Hymenoptera: Vespidae). *Insectes Soc* 42:17–29

O'Donnell S (1996) Reproductive potential and division of labor in wasps: are queen and worker behavior alternative strategies? *Ethol Ecol Evol* 8:305–308

O'Donnell S (1998a) Dominance and polyethism in the eusocial wasp *Mischocyttarus mastigophorus* (Hymenoptera: Vespidae). *Behav Ecol Sociobiol* 43:327–331

O'Donnell S (1998b) Effects of experimental forager removals on division of labor in the primitively eusocial wasp *Polistes instabilis* (Hymenoptera: Vespidae). *Behaviour* 135:173–193

O'Donnell S (1998c) Reproductive caste determination in eusocial wasps (Hymenoptera: Vespidae). *Annu Rev Entomol* 43: 323–346

- O'Donnell S (1999) The function of male dominance in the eusocial wasp, *Mischocyttarus mastigophorus* (Hymenoptera: Vespidae). *Ethology* 105:273–282
- O'Donnell S, Jeanne RL (1995a) Worker lipid stores decrease with outside-nest task performance in wasps: implications for the evolution of age polyethism. *Experientia* 5:749–752
- O'Donnell S, Jeanne RL (1995b) Implications of senescence patterns for the evolution of age polyethism in eusocial insects. *Behav Ecol* 6: 269–273
- O'Donnell S, Joyce FJ (2001) Seasonality and colony composition in the tropical eusocial wasp *Mischocyttarus mastigophorus* Richards (Hymenoptera: Vespidae). *Biotropica* (in press)
- Pardi L (1948) Dominance order in *Polistes* wasps. *Physiol Zool* 21:1–13
- Röseler PF (1991) Reproductive competition during colony establishment. In: Ross KG, Matthews RW (eds) *The social biology of wasps*. Cornell University Press, Ithaca, pp 309–335
- Röseler PF, Röseler I, Strambi A (1980) The activity of corpora allata in dominant and subordinated females of the wasp *Polistes gallicus*. *Insectes Soc* 27:97–107
- Röseler PF, Röseler I, Strambi A, Augier R (1984) Influence of insect hormones on the establishment of dominance hierarchies among foundresses of the paper wasp, *Polistes gallicus*. *Behav Ecol Sociobiol* 15:133–142
- Röseler PF, Röseler I, Strambi A (1985) Role of ovaries and ecdysteroids in dominance hierarchy establishment among foundresses of the primitively social wasp, *Polistes gallicus*. *Behav Ecol Sociobiol* 18:9–13
- Rossi AM, Hunt JH (1988) Honey supplementation and its developmental consequences: evidence for food limitation in a paper wasp, *Polistes metricus*. *Ecol Entomol* 13:437–442
- Sinha A, Premnath S, Chadrashekara K, Gadagkar R (1993) *Ropalidia rufoplagiata*: a polistine wasp society probably lacking permanent reproductive division of labour. *Insect Soc* 40:69–86
- Sokal RF, Rohlf FJ (1981) *Biometry*. Freeman, New York
- Strassmann JE, Meyer DC (1983) Gerontocracy in the social wasp, *Polistes exclamans*. *Anim Behav* 31:431–438
- Turillazzi S, Turillazzi CM (1985) Notes on the social behaviour of *Ropalidia fasciata* (F.) in West Java (Hymenoptera Vespidae). *Monit Zool Ital* 19:219–230
- West-Eberhard MJ (1969) The social biology of polistine wasps. *Misc Publ Mus Zool Univ Mich* 140:1–101
- West-Eberhard MJ (1981) Intragroup selection and the evolution of insect societies. In: Alexander RD, Tinkle DW (eds) *Natural selection and social behavior: recent research and new theory*. Chiron, New York, pp 3–17
- Wheeler DE (1994) Nourishment in ants: patterns in individuals and societies. In: Hunt JH, Nalepa CA (eds) *Nourishment and evolution in insect societies*. Westview Press, Boulder, pp 245–278
- Wheeler DE, Martinez T (1995) Storage proteins in ants (Hymenoptera: Formicidae). *Comp Biochem Physiol* 112B:15–19