

Research article

Food supplementation affects colony-level life history traits in the annual social wasp *Polistes metricus* (Hymenoptera, Vespidae)

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Received 30 June 2003; revised 9 December 2003; accepted 18 December 2003.

Summary. A field population of *Polistes metricus* Say near St. Louis, Missouri was supplemented with dilute *Apis mellifera* honey and *Trichoplusia ni* caterpillars during the entire colony development period. Offspring were collected at two times to coincide with emergence of worker and reproductive broods. Food supplementation had no effect on nest size, the number of worker offspring, or the size of workers. Supplemented colonies did produce more females in August but female size was unaffected by supplementation. Supplementation had no effect on the number of males produced, but males were slightly larger on supplemented nests. We interpret these findings in the context of social insect life history theory.

Key words: Annual life cycle, food supplementation, life history, *Polistes*, sex ratio.

Introduction

A fundamental problem facing annual species in seasonal environments is achieving reproductive success in one season. If a given year is suboptimal, they cannot forgo reproduction until the following year. Although life histories are thought to reflect the optimal partitioning of resources among competing demands, or tradeoffs (Stearns, 1992), little is known about how resource availability affects allocation patterns in annual social insects. Life history models for annual plants and for social insects living in seasonal environments suggest that the optimal life history strategy delays sexual reproduction as long as possible while building up reserves that will eventually help to produce the largest amount of propagules late in the season (Oster and Wilson, 1978; Schaal and Leverich, 1981; Bourke and Franks, 1995). In support of this notion are studies on the annual wasp *Polistes metricus* Say that suggests that pre-emergence phase colonies are food limited (Rossi and Hunt, 1988), but demo-

graphic consequences do not become evident until later in the colony cycle when sexuals are produced (Hunt and Dove, 2002). Nests supplemented before worker emergence attained larger sizes and produced more pupae in August when the sexuals emerge than did unsupplemented nests or nests from which larval saliva was removed (Hunt and Dove, 2002). Unclear, however, is how food supplementation might affect the partitioning among competing demands (worker, gyne or male production). Here we report effects of food supplementation on the number, size, and sex of adult offspring produced in the worker and reproductive broods in field colonies of *P. metricus* during an entire colony development period.

Materials and methods

This study was conducted in eastern Missouri at Weldon Spring Conservation Area (38.7°N, 90.7°W) and at Washington University's Tyson Research Center (38.5°N, 90.55°W) from April through August 1997. Both sites are characterized by patches of second growth oak-hickory forest interspersed with fields. *Polistes metricus* is a common species in this habitat and readily founds nests in man-made nest boxes. This species is also haplometrotic (Hunt and Dove, 2002), which means that nests are initiated by single foundresses (Reeve, 1991). Typically the workers in this population emerge by early July and the reproductives by mid-August (Hunt and Dove, 2002). Although castes are not dimorphic, the production of larger females in August (Seal, unpubl. data) along with males indicates that colonies are in the reproductive phase.

In early March 1997, prior to nest founding, we placed 60 (10 × 10 × 10 cm) nest boxes in fields at each study site. After foundresses appeared in boxes and began to make nests, we haphazardly assigned each colony to a collection time (July or August) and one of two treatments: 1) supplementation with dilute *Apis mellifera* honey and *Trichoplusia ni* (Lepidoptera, Noctuidae) caterpillars, or 2) no supplementation but equal amounts of disturbance. Before the treatments commenced the nests had the same number of cells ($F_{1,21} = 0.0163$, $p > 0.85$). The honey supplementation augments naturally occurring wasp honey that is commonly found in *P. metricus* nests in the beginning and later phases of the colony cycle (Hunt et al., 1982, 1998; Hunt, 1991). Honey treatments began immediately following nest founding. Honey was applied twice weekly to the edge of every other nest cell, out of reach of

the larvae, as described in Rossi and Hunt (1988) and Hunt and Dove (2002). Caterpillar supplementation augments the natural source of protein for wasp brood and commenced with the appearance of second instar larvae (approx. June 1). Colonies were fed twice weekly by feeding a piece of mashed caterpillar to the foundress directly or placing the food on top of the nest comb. The size of this caterpillar morsel approximated the amount of prey wasps were seen transporting back to their nest and was supplied at the rate of one caterpillar per worker found on the nest. Treatments continued until nests were removed from the field.

In late June, after the appearance of pupal cocoons, the first group of nests, minus the foundresses, were removed from the nest boxes and taken from their field location. These nests were placed in a remote shaded outdoor location, and each was covered by a transparent plastic cup. Nest size and the numbers of pupae, larvae, and eggs were recorded. As adults emerged from pupation they were placed in vials, labeled, and killed by freezing. The isolation and offspring collection procedure was repeated for the August sample. We estimated the size of offspring by taking seven body measurements of each wasp (Jeanne et al., 1995; Hunt et al., 1996, 2001): G1AW (apical width of the first gastral segment); G1L (length of the first gastral segment); G2W (width of the second gastral segment); HH (head height); HW (head width); TL (thorax length); TW (thorax width); and WL (wing length). Measurements were made, with a binocular microscope equipped with a video camera.

Treatment effects were assessed by analysis of covariance with the numbers of offspring as the dependent variable, cell size as a covariate, and treatment as a categorical predictor. The numbers of offspring corresponded to the exact number of wasps used in the morphometric analysis. All data were common log transformed in order to meet parametric assumptions. The sex ratio was analyzed by performing a t-test on the percentage of sexual offspring allocated to males and by performing a Chi-Square test on the frequencies of adult August offspring. The size of offspring was analyzed with simple non-parametric Mann-Whitney tests, because of unequal variance terms. All statistical analyses were performed with Statistica version 6.1 (Statsoft, 2003).

Results

Food supplementation had no effect on the worker (July) brood. The number of wasps produced was unrelated to nest size ($r = 0.05$, $p > 0.85$), nor did it appear to be related to treatment ($F_{1,10} = 1.03$, $p > 0.33$). Worker size for each colony was not significantly affected by food supplementation.

Food supplementation significantly increased the number of females in the August brood ($F_{1,7} = 11.82$, $p < 0.01$, Fig. 1) and larger nests produced slightly more female offspring ($r^2 = 0.24$, $F_{1,7} = 5.65$, $p < 0.05$, Fig. 1). The treatment did not appear to significantly affect female body size or the numbers of males produced on nests in August ($F_{1,7} = 0.362$, $p > 0.55$). In contrast to female sexual brood, the male number and nest size were positively correlated ($r = 0.91$, $p < 0.001$). Additionally, males on supplemented nests were significantly larger in the thorax width and the apical width of the first gastral segment (Table 1). Supplemented nests produced about 50% fewer males (0.416 ± 0.102) (average male allocation ± 1 sd) compared to unsupplemented nests (0.628 ± 0.154 , $t_{df=8} = 2.405$, $p < 0.05$). In supplemented colonies the number of males did not differ from the expected number in a 1:1 ratio ($\chi^2 = 1.61$, 3 df, $p > 0.60$), whereas in unsupplemented colonies the number of males did not differ from a 3:1 (male:female) ratio ($\chi^2 = 3.96$, 5 df, $p > 0.55$).

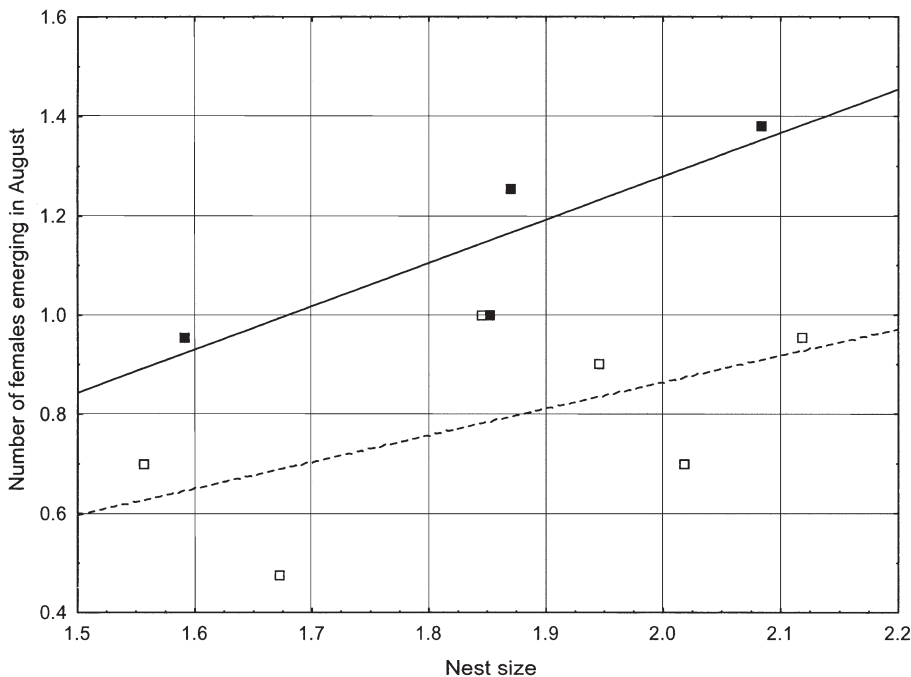


Figure 1. Number of *Polistes metricus* female offspring as a function of nest size for colonies collected during the reproductive production phase of the colony cycle. Solid symbols are supplemented colonies and open symbols are unsupplemented. Data are log transformed

Table 1. Measurements (means \pm standard deviations in mm) of eight body dimensions of male offspring of supplemented and unsupplemented colonies (Mann-Whitney U test). Significant differences ($\alpha = 0.05$) are highlighted in bold. $n_{\text{control}} = 5$, $n_{\text{supp}} = 4$

Measurement	Unsupplemented	Supplemented	Z	p-value
HH	3.202 (.091)	3.265 (.068)	0.980	0.327
HW	3.288 (.118)	3.405 (.072)	1.715	0.087
TL	5.192 (.242)	5.405 (.113)	1.470	0.142
TW	2.992 (.088)	3.11 (.085)	1.96	0.05
G1AW	3.064 (.027)	3.275 (.138)	2.45	0.014
G1L	2.77 (.179)	2.888 (.074)	1.47	0.142
G2W	3.944 (.119)	4.088 (.117)	1.59	0.11
WL	8.898 (.710)	9.093 (.088)	0.49	0.624

Discussion

This study reaffirms the finding by Hunt and Dove (2002) that food supplementation of field colonies of *Polistes metricus* affects later stages of colony development. Neither the number nor the sizes of worker offspring appear to have been affected by the food supplementation, which suggests that there may be little adaptive advantage to creating more or larger workers. It appears that there could be stabilizing selection to produce a relatively fixed number of workers regardless of nest size or food availability. The food supplement appears to have been shifted toward the production of a greater number of female sexuals and larger males. That supplemented colonies produced more reproductive females rather than larger reproductive females suggests that female sexual production in natural conditions is food limited and possibly expensive. These results are also in agreement with Karsai and Hunt (2002) who found little relationship between food supplementation and female offspring size.

Metcalf (1980) argued that *P. metricus* colonies were likely to invest equally in males and females, but he did not consider physiology. Gynes are likely to be more expensive to produce than males or workers, because gynes require more body fat (Eickwort, 1969; Strassmann et al., 1984), more protein (Hunt et al., 2003) and anti-freeze compounds (Gibo, 1976; Strassmann et al., 1984) during their dormant period and subsequent nest founding. Protection against freezing involves the conversion of the insect's entire glycogen supply into polyols that lower the super-cooling point of water and the synthesis of large molecular weight ice nucleating proteins (Duman and Patterson, 1978; Storey, 1990). This process is metabolically expensive; queens of the temperate vespine *Dolichovespula maculata* were found to lose >80% of their glycogen reserves during hibernation (Stein and Fell, 1992). Since Karsai and Hunt (2002) found that worker *P. metricus* have a lower freezing tolerance than gynes and cold tolerance of female offspring is positively correlated with the amount of food received as a larva, it seems likely that anti-freeze compounds represent a significant cost in *P. metricus* as well. Karsai and Hunt (2002) also found that colonies receiving more food delayed the production of males by investing in females. Experimental studies investigating the physiological costs of rearing worker, reproductive, or male brood in *Polistes* wasps could contribute significantly to our understanding of this pattern.

Our results can be readily interpreted in the context of life history theory developed for plants, because plants and social insects exhibit many parallels in terms of their development and demography (Harper, 1977; Hunt, 1991; Bourke and Franks, 1995). The finding that female *P. metricus* wasp size appeared to be unaffected by extra food, but their number was, supports theory predicting that selection has yielded an optimal investment in sexual quality and that colonies accrue fitness when they produce more offspring that are relatively equal in quality (Lloyd, 1987). For example, larger plant seeds appear to be advantageous when seedlings are likely to experience competition, but in the absence of competition, the best strategy would be to produce many smaller seeds (Sibly et al., 1988; Bourke and Franks, 1995; Turnbull et al., 1999). Similarly, social wasp (*Dolichovespula maculata* (L.)) foundresses exhibited little inter-annual variation in size or nutrient reserves (Stein and Fell, 1992). Although large *Polistes* foundresses are generally favored in encounters with conspecifics during nest usurpation attempts or in foundress associations (Reeve, 1991), size is probably unimportant in our population since foundress associations are very rare (JHH, unpubl. data). Instead, survivorship appears to be dependent on density-independent factors during winter diapause and the subsequent nest-founding season. Only 2 of more than 600 wasps individually marked at a single field site in 1994 appeared the following year (Hunt and Dove, 2002). Colony mortality in *P. metricus* appears to be fairly steady throughout the colony cycle driven by random parasite and predator attacks (Hunt and Dove, 2002; Hodges et al., 2003), as is reported in other species of *Polistes* (Page et al., 1989; Clapperton and Dymock, 1997). *Polistes metricus* colonies thus appear to produce female offspring that are relatively equal in quality but variable in number depending on the amount of food the colony receives.

Our finding that supplementation results in slightly larger males rather than a greater number of males suggests that the number of males produced by a colony may not be as important a fitness variable as male size. Reed and Landolt (1991) noted lekking of sexuals of *P. metricus* with males forming large swarms. We have observed similar behavior in *P. metricus* on goldenrod (*Solidago* spp.) inflorescences. Males appear to patrol these flowers and attack other males that come near (pers. obs.). Since lekking has additionally been reported or suggested in several species of *Polistes* (Lin,

1972; Noonan, 1978) and larger males appear to defend territories (Polak, 1993), it is possible that larger *P. metricus* males have higher fitness.

Acknowledgements

This study was supported in part by a Marlin Perkins Fellowship to JNS and an UM-St.Louis Research Award to JHH. Owen Sexton and the staff of Tyson Research Center and Dan Crigler of the Missouri Department of Conservation allowed us to work on land in their care. Jon H. and Karen Seal kindly allowed the use of their woodshed as an outdoor vesparium and Maria Guerrero assisted with data collection. We also thank the comments of two anonymous reviewers that helped us improve this manuscript.

References

- Bourke, A.F.G. and N.R. Franks, 1995. *Social Evolution in Ants*. Princeton University Press, Princeton, New Jersey. 529 pp.
- Clapperton, B.K. and J.J. Dymock, 1997. Growth and survival of colonies of the Asian paper wasp, *Polistes chinensis antennalis* (Hymenoptera: Vespidae), in New Zealand. *N.Z. J. Zool.* 24: 9–15.
- Duman, J.G. and J.L. Patterson, 1978. The role of ice nucleators in the frost tolerance of overwintering queens of the Bald Faced Hornet. *Comp. Biochem. Physiol.* 59A: 69–72.
- Eickwort, K., 1969. Separation of castes of *Polistes exclamans* and notes on its biology (Hym.: Vespidae). *Insect. Soc.* 16: 67–72.
- Gibo, D.L., 1976. Cold hardiness in fall and winter adults of the social wasp *Polistes fuscatus* (Hymenoptera: Vespidae) in southern Ontario. *Can. Entomol.* 108: 801–806.
- Harper, J.L., 1977. *Population Biology of Plants*. Academic Press, San Diego, California. 892 pp.
- Hodges, A.C., G.S. Hodges and K.E. Espelie, 2003. Parasitoids and parasites of *Polistes metricus* Say (Hymenoptera: Vespidae) in north-east Georgia. *Ann. Entomol. Soc. Am.* 96: 61–64.
- Hunt, J.H., 1991. Nourishment and the evolution of the social Vespidae. In: *The Social Biology of Wasps* (K.G. Ross and R.W. Matthews, Eds). Cornell University Press, Ithaca, NY, USA. pp. 426–450.
- Hunt, J.H., I. Baker and H.G. Baker, 1982. Similarity of amino-acids in nectar and larval saliva – the nutritional basis for trophallaxis in social wasps. *Evolution* 36: 1318–1322.
- Hunt, J.H., N.A. Buck and D.E. Wheeler, 2003. Storage proteins in vespid wasps: characterization, developmental pattern and occurrence in adults. *J. Insect Physiol.* 49: 785–794.
- Hunt, J.H. and M.A. Dove, 2002. Nourishment affects colony demographics in the paper wasp *Polistes metricus*. *Ecol. Entomol.* 27: 467–474.
- Hunt, J.H., S. O'Donnell, N. Chernoff and C. Brownie, 2001. Observations on two neotropical swarm-founding wasps, *Agelaia yepocapa* and *A. panamaensis*. *Ann. Entomol. Soc. Am.* 94: 555–562.
- Hunt, J.H., A.M. Rossi, N.J. Holmberg, S.R. Smith and W.R. Sherman, 1998. Nutrients in social wasp (Hymenoptera: Vespidae, Polistinae) honey. *Ann. Entomol. Soc. Am.* 91: 466–472.
- Hunt, J.H., D.K. Schmidt, S.S. Mulkey and M.A. Williams, 1996. Caste dimorphism in the wasp *Epipona guerini* (Hymenoptera: Vespidae; Polistinae, Epiponini): Further evidence for larval determination. *J. Kansas Entomol. Soc.* 69: 362–369.
- Jeanne, R.L., C.A. Graf and B.S. Yandell, 1995. Non-sized base morphological castes in a social insect. *Naturwissenschaften* 82: 296–298.
- Lin, N., 1972. Territorial behavior among males of social wasp *Polistes exclamans* Viereck – (Hymenoptera-Vespidae). *Proc. Entomol. Soc. Wash.* 74: 148–155.
- Lloyd, D.G., 1987. Selection of offspring size at independence and other size- versus-number strategies. *Am. Nat.* 129: 800–817.
- Metcalf, R.A., 1980. Sex ratios, parent offspring conflict, and local competition for mates in the social wasps *Polistes metricus* and *Polistes variatus*. *Am. Nat.* 116: 642–654.
- Noonan, K.M., 1978. Sex ratio of parental investment in colonies of the social wasp *Polistes fuscatus*. *Science* 199: 1354–1356.
- Oster, G.F. and E.O. Wilson, 1978. *Caste and Ecology in the Social Insects*. Princeton University Press, Princeton, New Jersey. 352 pp.
- Page, R.E., D.C. Post and R.A. Metcalf, 1989. Satellite nests, early males, and plasticity of reproductive behavior in a paper wasp. *Am. Nat.* 134: 731–748.
- Polak, M., 1993. Competition for landmark territories among male *Polistes canadensis* (L) (Hymenoptera, Vespidae): large-size advantage and alternative mate-acquisition tactics. *Behav. Ecol.* 4: 325–331.
- Reed, H.C. and P.J. Landolt, 1991. Swarming of paper wasp (Hymenoptera: Vespidae) sexuals at towers in Florida. *Ann. Entomol. Soc. Am.* 84: 628–635.
- Reeve, H.K., 1991. *Polistes*. In: *The Social Biology of Wasps* (K.G. Ross and R.W. Matthews, Eds). Cornell University Press, Ithaca, NY, USA. pp. 99–148.
- Rossi, A.M. and J.H. Hunt, 1988. Honey supplementation and its developmental consequences – evidence for food limitation in a paper wasp, *Polistes metricus*. *Ecol. Entomol.* 13: 437–442.
- Schaal, B.A. and W.J. Leverich, 1981. The demographic consequences of two stage life cycles: survivorship and the time of reproduction. *Am. Nat.* 118: 135–138.
- Sibly, R., P. Calow and R.H. Smith, 1988. Optimal size of seasonal breeders. *J. Theor. Biol.* 133: 13–21.
- Statsoft, I., 2003. STATISTICA (data analysis software system) Version 6.1. Tulsa, Oklahoma, USA.
- Stearns, S.C., 1992. *The Evolution of Life Histories*. Oxford University Press, New York. 249 pp.
- Stein, K.J. and R.D. Fell, 1992. Seasonal comparison of weight, energy reserve, and nitrogen changes in queens of the baldfaced hornet (Hymenoptera: Vespidae). *Environ. Entomol.* 21: 148–155.
- Storey, K.B., 1990. Biochemical adaptation for cold hardiness in insects. *Phil. Trans. R. Soc. London B.* 326: 635–654.
- Strassmann, J.E., R.E. Lee Jr., R.R. Rojas and J.G. Baust, 1984. Caste and sex differences in cold-hardiness in the social wasps, *Polistes annularis* and *P. exclamans* (Hymenoptera: Vespidae). *Insect. Soc.* 31: 291–301.
- Turnbull, L.A., M. Rees and M.J. Crawley, 1999. Seed mass and the competition/colonization trade-off: a sowing experiment. *J. Ecol.* 87: 899–912.