J Ethol (2012) 30:201–204
DOI 10.1007/s10164-011-0298-5

SHORT COMMUNICATION

A trade-off between number and size within the first workers of the ant *Camponotus japonicus*

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Received: 1 March 2011 / Accepted: 10 August 2011 / Published online: 4 September 2011

Abstract In social insects, the limited amount of resources during the claustral founding predicts a trade-off between the number and size of the first-generation of workers. Here, we demonstrate this predicted trade-off in founding colonies of the ant *Camponotus japonicus*. Worker size was found to correlate negatively with the number of first workers produced when the amount of investment was controlled. Both size and number of the first generation of workers increased when a queen invested more resources. We also examined how a queen adjusts the size and number of the first workers depending on her condition.

Keywords Trade-off · Founding colony · Social insect · Ant · *Camponotus japonicus*

Introduction

A trade-off between characters is a key factor that shapes the adaptations made by organisms (Krebs and Davies 1997). In social insects, the first generation of workers are usually much smaller than those in more mature colonies (Wilson 1971; Porter and Tschinkel 1985, 1986; Miyano 1990; Hasegawa 1993). The ergonomic theory of social insects explains this phenomenon as a result of a trade-off between number and size within the first brood of workers because the amount of resources available during colony founding is very limited (Oster and Wilson 1978). The rationale of this theory is: (1) for a founding queen, a limited amount of resources is available to rear the first brood; (2) large workers are more efficient in task processing but a minimum number of workers is required to ensure survival; (3) these ambivalent constraints lead to a trade-off between number and size of the first brood of workers, resulting in the first workers being much smaller size than those in more mature colonies.

Ants show several modes of colony founding, such as claustral (without foraging by the queen), semi-claustral (with foraging by the queen), and budding (queen dispersal with workers). Claustral ants are suitable organisms for examining none the trade-off between size and number of the first brood of workers because only the stored resources in the queen's body are available to produce this first brood. Thus, important parameters in trade-off studies, such as initial weight and size of queens, invested amount of resources to the first workers, and size and number of the first workers, can be studied in claustral ants.

Earlier studies have shown that small first-generation worker ants of *Solenopsis invicta* can produce more second-generation workers than the same mass (=fewer worker ants) of large workers (Porter and Tschinkel 1986). The authors of these studies also showed that the large first-generation workers can rear more second-generation workers than the same numbers of smaller first-generation workers (Porter and Tschinkel 1985). These results predict that there is a trade-off between size and number in first workers under a resource limitation. In addition, a queen is predicted to produce many large workers when she has enough resources. Just how a queen alters resource allocation to size and number depending on her condition is another interesting issue.

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A study on *Camponotus japonicus* revealed that number of first-generation workers correlated positively with the queen's initial weight (Liu et al. 2001), with an additional food supply increasing the number of the first workers (Liu et al. 2001). However, no study to date has shown the presence of a trade-off between size and numbers within first-generation workers in social insects.

In this study, we measured several ecological parameters of founding colonies in the ant *Camponotus japonicus*. The predicted trade-off is examined by showing relationships among size, numbers, and invested resources. We also examined condition-dependent resource allocation to size and numbers by comparing regression slopes of size and number to conditional parameters of the queens.

Materials and methods

After a mass nuptial flight of *C. japonicus*, we collected 26 dealated queens on the ground on 3 June 1999 at Sankakuyama, Sapporo, Japan. The live weight of each queen was recorded within the collection day. Each queen was reared in a petri dish (diameter 9 cm, depth 9 mm) with water supply. No additional food was supplied. The queens were kept under a dark condition at room temperature (19–24°C). The number of eggs, larvae, pupae, and eclosed workers were counted daily. Live weight and head width of the queen (HQ) were measured when the last pupa had been eclosed (approx. 2 months later), and the head width of each worker (HW) was also measured. Each queen's investment in the first generation of worker ants was estimated as the difference in live weight between the collection day and the final measurement. Additional parameters measured were number of first-generation workers (NW), investment of a queen in her first workers (IQ), and initial live weight of a queen (IWQ). Relationships among the parameters were examined by simple and partial correlations. In order to evaluate the effect of outliers on correlation coefficients, for all of the first broods, we examined the deviation from normality of the distribution of HW by using the skewness and kurtosis. We also conducted a jack-knife estimation of the standard error (SE) for the partial correlation coefficients. In this estimation, the correlation is not different from zero if there is a positive (or negative) correlation due to the appearance of an extraordinary value attributable to a colony.

Condition-dependent allocations were examined by regression analyses using standardized data. Standardized NW and HW were regressed on the following conditional parameters of the queens: IQ/IWQ (investment per unit weight), IQ/HQ (investment per unit size), and IWQ/HQ (initial fatness). Each conditional parameter was also standardized. All statistics were calculated using computer software R, ver. 2.92; R Development Core Team, Vienna, Austria).

Results

The queens laid the first batch of eggs [26.4 ± 1.7, average ± standard deviation (SD)] within approximately 10 days; thereafter, the eggs did not increase in number. Three queens failed to produce first-generation workers: one did not lay eggs, one died during the rearing period and one produced pupae which did not eclose. As a result, data were obtained none for 23 colonies. Average values of the measured parameters were: NW = 10.5 ± 1.3 (average ± SD), HW = 1.16 ± 0.02 mm, HQ = 3.15 ± 0.15 mm, IWQ = 121.1 ± 9.2 mg, and IQ = 59.7 ± 7.1 mg.

The results of the partial correlation analyses are summarized in Table 1. NW was negatively correlated with HW when IQ was controlled ($r = -0.569$), while each NW or HW was positively correlated with IQ when the remaining variables were controlled ($r = 0.851$ and 0.575, respectively). There was no significant correlation between HQ and IQ ($r = 0.235$). HQ showed no significant correlation with HW in the simple correlation and partial correlations when IQ or IQ + NW was controlled ($r = 0.147$, 0.102, and 0.022, respectively).

For all broods, there was no significant deviation from normality (skewness: $b1 = -0.00099$ to 0.00140, $p > 0.05$ for all values; kurtosis: $b2 = 0.00004$–0.00024, $p > 0.05$ for all values). These results indicate that the HW was normally distributed in all of the colonies. In addition, all of the jack-knifing correlations were significantly different from zero, suggesting that the correlation coefficient based on the whole data set was not affected by an outlier. Both results suggest that outliers did not affect our results.

For IQ/IWQ, NW showed a significantly steeper slope than HW (Fig. 1a; $t = 2.099$, $df = 42$, $p = 0.021$). The

Table 1 Correlations between productive parameters of a founding colony of *Camponotus japonicus*

Correlated variables	Controlled variable(s)	r	t_0	p
NW versus HW	IQ	−0.569	3.0944	0.0057
NW versus IQ	HW	0.851	7.2468	0.0000051
HW versus IQ	NW	0.575	3.1430	0.0051
HQ versus IQ	–	0.235	1.0812	0.2924
HQ versus HW	–	0.147	0.6810	0.5029
HQ versus HW	IQ	0.102	0.4585	0.6515
HQ versus HW	IQ, NW	0.022	0.0959	0.9246

NW Number of first-generation workers, *IQ* investment of a queen in her first-generation workers, *HQ* head width of queen, *HW* average head width of the first generation of workers of a queen

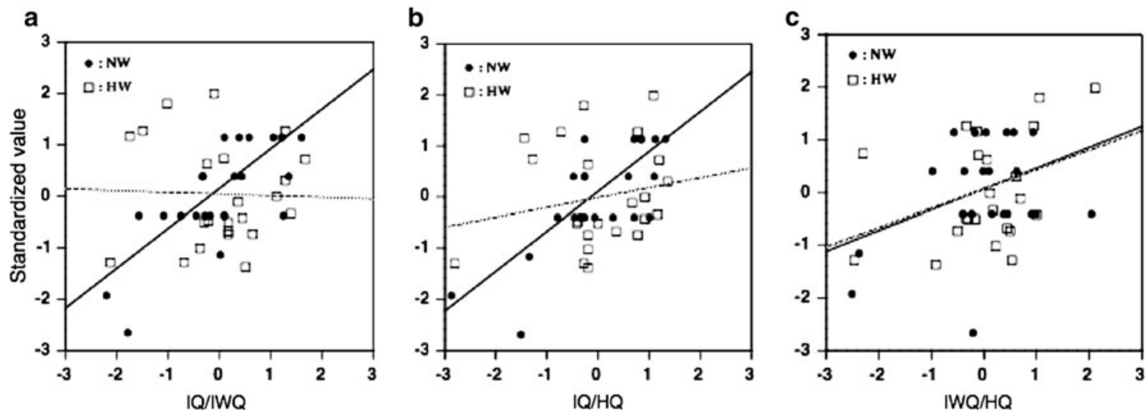

Fig. 1 Regressions of the standardized number of first-generation workers (NW; *closed circle*) and average head width of the first-generation workers (HW; *open square*) on the proportion of investment of the queen in her first workers to the initial weight of the queen (*IQ/IWQ*; **a**), on the IQ per width (size) of queen's head (*IQ/HQ*; **b**), and the initial condition (weight) of the queen per queen's HQ (*IWQ/HQ*; **a**). *Solid* and *dotted lines* Regression lines for NW and HW, respectively

slope of NW was significant ($b = 0.738$, $t = 5.007$, $df = 21$, $p = 0.000010$), but that of HW was not different from zero ($b = -0.032$, $t = -0.147$, $df = 21$, $p = 0.884$). A similar trend was observed for IQ/HQ (NW: $b = 0.757$, $t = 5.319$, $df = 21$, $p = 0.000028$; HW: $b = 0.159$, $t = 0.733$, $df = 21$, $p = 0.465$) but the difference between the slopes was not significant although the p value was close to 0.05 ($t = 1.994$, $df = 42$, $p = 0.053$). For IWQ/HQ, both NW and HW showed similar slopes ($b = 0.351$ and 0.369, respectively), and the difference between them was not significant ($t = 0.941$, $df = 42$, $p = 0.176$).

Discussion

The results of this study clearly show that there is a trade-off between the number and size within the first generation of *C. japonicus* workers. When IQ was controlled, there was a negative partial correlation between NW and HW (Table 1). This trade-off is predicted if the available resources are less than the amount required to simultaneously realize both the optimal number and size of workers (Oster and Wilson 1978). In the ant *S. invicta*, large workers have been shown to be more efficient than small workers under the condition of equal numbers, but to be less efficient under the condition of equal mass (Porter and Tschinkel 1985, 1986). These results indicate that the small size of the first-generation workers is a suboptimal trait. In many social insects, the first brood of workers produced during the colony founding is much smaller than workers in mature colonies (Wilson 1971; Miyano 1990; Hasegawa 1993). The claustral founding mode of ants limits available resources for production of the first brood according to the stored resources in the queen's body. There is a possibility that the observed trade-off can be attributed to the negative genetic correlations between NW and HW. However, it is difficult to discriminate between resource limitation and negative genetic correlation as the main cause of the realized trade-off (Charlesworth 1990; Houle 1991). In addition, a degree of genetic variance among workers affects colony ergonomics in social insects (Johnson and Linksvayer 2010). Monogynous *Camponotus* species seem to have fewer genetic variances within workers due to the single mating of the queen (Hasegawa 1993). Thus, although further studies are required to evaluate the relative contribution of the two factors, a strong limitation of resources seems to lead to the dwarfism and the trade-off between the number and size in the first-generation workers in *C. japonicus*.

The obtained positive partial correlations between IQ and NW or HW (Table 1) also supported the above view. This result is consistent with a previous result in which the numbers of first-generation workers correlated positively with the investment made in them (Liu et al. 2001). However, our study primarily showed that worker size is also correlated with the investment in first-generation workers. The observed correlations indicate that a queen attempts to produce both larger numbers and larger sizes of first-generation workers when she stores a large amount of resources. When there is the predicted trade-off, the realized number and size of the first generation of workers might be a compromise. Thus, a queen benefits from producing large and many workers if there is a sufficient amount of resources.

Although a large queen may be able to store more resources than a small queen, HQ was not correlated with IQ (Table 1). In *C. japonicus*, alates are produced in the previous summer and overwinter in the nest. In *Camponotus* (*Colobopsis*) *nipponicus*, females store additional nutrients after eclosion (Hasegawa 1994). These results suggest that the available amount of resources is affected by resource availability after eclosion. Unpredictable resource conditions might be the cause of the lack of the correlation.

The correlation of HQ with HW was not significant in the simple and partial correlations when IQ or both IQ and NW was controlled (Table 1), suggesting that the size of the first-generation workers does not correlate genetically with the queen's size. This conclusion may be reasonable because workers in mature colonies are much larger than the first-generation workers. In social insects, condition-dependent size determination is common (Wilson 1971; Hölldobler and Wilson 1990; but see Fjerdingstad 2005). Thus, the size of the first-generation workers in *C. nipponicus* would depend mainly on environmental factors.

How does a queen alter the resource allocation to NW and HW depending on her condition? Our analysis shows that NW responds positively to each of the conditional parameters (Fig. 1). However, the response of HW differs among the parameters (Fig. 1). Thus, although there is a negative partial correlation between NW and HW (Table 1), these variables responded differently to the queen's conditions. Despite this result, the negative partial correlation between NW and HW is not affected by condition-dependent allocation since the regression slopes are not different for the initial condition of a queen (IWQ/HQ). Further analyses are required to elucidate factors that determine different responses of NW and HW to IQ/IWQ or IQ/HQ.

In conclusion, our results confirm the several predictions of the ergonomic theory on a founding colony of social insects. The observed trade-off between number and size within the first generation of workers suggests that the realized size is a compromise. The consequence of this compromise is that the number and size of first-generation workers are flexible, changing in accordance with environmental factors (Liu et al. 2001). Thus, founding colonies of social insects are useful subject material for examining an evolutionary question: just how does queen adjust productive parameters to maximize her fitness under constraints?

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