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RESEARCH ARTICLE

Morphological differences between extranidal and intranidal workers in the ant *Temnothorax rugatulus*, but no effect of body size on foraging distance

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Abstract Most ant genera are thought to have monomorphic workers, indicating perhaps a high degree of flexibility in task allocation, and the well-studied genus *Temnothorax* is an example of this. However, considerable size variation may exist between individuals. In addition, though workers can show flexible behavior, it has been shown that individuals may consistently differ in their task profiles. Here we test whether body size variation among workers affects foraging behavior. Two main hypotheses were tested: first, whether larger ants forage at greater distance from the nest, and second, whether larger individuals show a higher propensity to work outside of the nest. Our results showed that ant body size does not significantly affect foraging distance. However, larger ants were more likely to be found outside the nest. Though *Temnothorax* ants are a common model system, this is the first study demonstrating task allocation based on body size, which is fixed in adults. Our study suggests that particularly small species may have to be examined carefully for body size variation before concluding that body size is uniform and therefore irrelevant for task allocation.

Keywords Task allocation · Foraging · Size variation · *Temnothorax* · Behavioral castes

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Introduction

Foraging behavior in animals is often tightly optimized by natural selection, as it is one of the most critical behaviors in determining the fitness of an organism (Schoener, 1971). In many animal species, larger individuals forage greater distances (Shutler and Mullie, 1991; Roland and Taylor, 1997). This can be due to the fact that larger animals need a larger territory to collect sufficient resources for their larger body mass (McNab, 1963), or due to larger animals being faster and more robust, and thus more efficient at long-distance foraging (Brooks and Dodson, 1965; Hassrick, et al., 2013). Differences in body size within species, or even within social insect colonies, may make certain individuals more suited at particular tasks other than foraging as well (Wilson, 1980a, 1984; Keiser, et al., 2014).

Some social insects have therefore evolved morphologically differing worker castes, the members of which are then allocated preferentially to different tasks (Pie and Traniello, 2007; Couvillon, et al., 2010; Jandt and Dornhaus, 2009). Most often, larger workers preferentially forage for resources, including food, water and potential nest locations (Wetterer, 1999; Jandt and Dornhaus, 2009; Wilson, 1980a; Hölldobler and Wilson, 1990), and are often more efficient at this task (e.g. Wilson, 1980b; Spaethe and Weidenmüller, 2002). In addition, a relationship between body size and foraging distance has also been observed in the eusocial bees *Bombus terrestris* and the social sweat bee *Lasioglossum umbripenne* (Greenleaf, et al., 2007). In ants, the mean and maximum distance traveled by some seed dispersing species has been shown to positively increase as mean worker body size increases (Ness, et al., 2004).

However, most ant genera are considered monomorphic (Hölldobler and Wilson, 1990; Fjerdingstad and Crozier, 2006). *Temnothorax rugatulus*, for example, are widely

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considered to have a monomorphic worker caste (Rueppell and Kirkma, 2005). In such species, workers are usually assumed to be highly flexible in their behavior, although some individual differences in task preferences have been shown in *Temnothorax* (Dornhaus, 2008; Robinson, et al., 2009; Pinter-Wollman, et al., 2012). Despite being considered monomorphic and behaviorally flexible, some worker size variation also exists.

Here, we investigate whether workers of different body size (1) forage at different distances, and (2) whether worker body size affects the likelihood of foraging, in *Temnothorax rugatulus*.

Methods

Foraging distance was measured during October of 2010 and May of 2011 in the Santa Catalina Mountains (near Tucson, AZ, USA) for 20 different colonies (Bengston and Dornhaus, 2013). Colonies were located by setting baits and following extranidal workers (workers outside of the nest) from the baits to their colony, and then aspirating them into a collection container before re-entry into the nest to avoid recruitment of other workers. After a colony was located, the baits were removed, and any ants seen leaving were marked with pink fluorescent powder (to increase visibility to the observer) and followed. The farthest distance from the nest that each ant reached before turning back was measured ('foraging distance'). Each of these extranidal workers was collected separately and submerged in an 80 % ethanol solution in a 2 ml Eppendorf Tube®. After 18 (±3) extranidal workers were collected, the nest was opened and 10 (±1) ants from inside the nest were randomly selected and preserved in a similar manner. All preserved specimens were stored in the dark at room temperature (25 ± 2 °C) for a maximum of 3 months before they were measured.

The head width of each ant was measured under a light microscope with a micrometer to the nearest 0.05 mm. Head width is a standard measurement of body size in ants (Tschinkel, et al., 2003) as opposed to body length or gaster width which is affected by corpulence (Tschinkel, 2013). In total, 332 extranidal workers and 190 intranidal workers (those collected from inside the nest) were measured.

Statistical analysis was completed using Minitab Student 14 software, as well as 'R' statistical software, v2.14.2 with Tinn-R Editor graphic user interface. A correlation coefficient was used to see if foraging distance was related to worker body size. A generalized linear model (GLM) was used to look for colony effects on body size in relation to foraging distance, and a generalized linear mixed model (GLMM) was used to look for effect of location collected (extranidal or intranidal) and colony of origin on worker head size.

Results

No significant correlation was found between body size and foraging distance (Fig. 1; $P = 0.262$, $R^2 = 0.0036$, df = 343). Additionally, colony of origin also did not affect foraging distance (GLM; worker size: $P = 0.2013$, colony of origin = 0.1109). However, the head size of workers was predicted by the location of collection (inside or outside of the nest), with extranidal workers having significantly larger head size than the intranidal workers, though again there was no effect of colony of origin (avg. intranidal worker head width = 0.42 mm, avg. extranidal worker head width = 0.51 mm. GLMM: collection location as a fixed effect, colony of origin as a random effect. Location: $P = 0.0001$, colony of origin $P = 0.2330$) (Fig. 2). This suggests a morphological difference between workers performing different tasks.

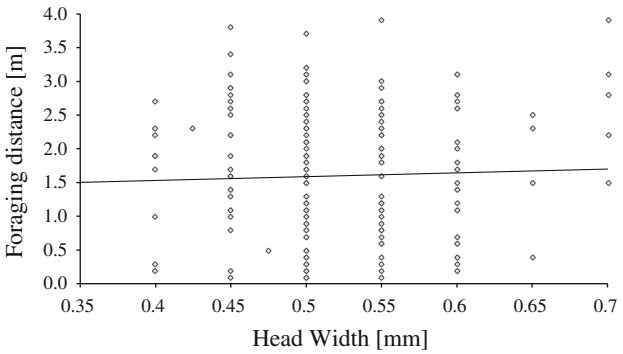

Fig. 1 The head size of each extranidal ant and the distance they traveled. All head size measurements were measured to the nearest 0.05 mm. Head size did not significantly correlate to distance traveled ($P = 0.262$, $R^2 = 0.0036$, df = 343)

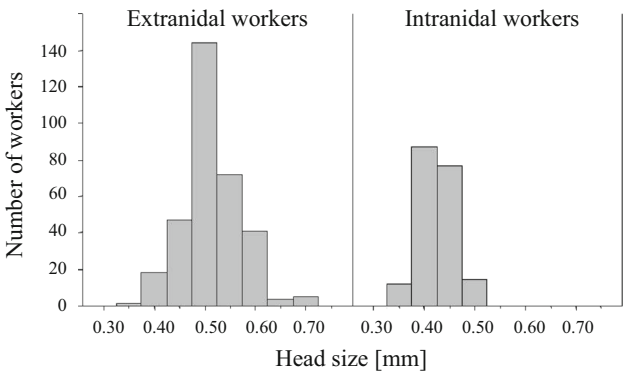

Fig. 2 The distribution of head sizes among extranidal workers ($n = 332$) and intranidal workers ($n = 190$). The two distributions have significantly different medians ($P < 0.0001$, median extranidal worker = 0.5 mm, median intranidal worker = 0.4 mm)

Discussion

In this study, we investigated the effect of worker body size in *Temnothorax rugatulus*. We document differences in body size between extranidal and intranidal workers. Foraging distance, however, was not affected by body size. Though corpulence (lipid storage) variation among workers, and its effect on foraging, has been well documented (Robinson, et al., 2009; Modlmeier, et al., 2012; Tschinkel, 2013), this study is the first to identify an effect of morphological body size variation on task allocation in *Temnothorax* ants, despite this genus being a popular model system for foraging and emigration studies within the lab.

Larger individuals in many species will travel further to forage for the necessary resources (Greenleaf, et al., 2007; Roland and Taylor, 1997). However, this does not seem to be the case in our study. As colony size also does not predict foraging distance, perhaps foraging distance in *Temnothorax rugatulus* is not under tight selection (Bengston and Dornhaus, 2013). Morphological variation has been closely tied to task differentiation across many eusocial insects (e.g. Pie and Traniello, 2007; Couvillon, et al., 2010). However, many, particularly small-bodied species, are thought to be monomorphic, i.e., not vary in body size enough to affect task allocation (Hölldobler and Wilson, 1990). Our study suggests that such species have to be studied in detail before an effect of body size on division of labor can be excluded.

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References

Bengston S.E. and Dornhaus A. 2013. Colony size does not predict foraging distance in the ant *Temnothorax rugatulus*: a puzzle for standard scaling models. *Insect. Soc.* **60**: 93–96

Brooks J.L. and Dodson S.I. 1965. Predation, body size, and composition of plankton. *Science* **150**: 28–35

Couvillon M.J., Jandt J.J., Duong N. and Dornhaus A. 2010. Ontogeny of worker body size distribution in bumblebee (*Bombus impatiens*) colonies. *Ecol. Entomol.* **35**: 424–435

Dornhaus A. 2008. Specialization does not predict individual efficiency in an ant. *Plos Biol*. **6**: 2368–2375

Greenleaf S.S., Williams N.M., Winfree R. and Kremen C. 2007. Bee foraging ranges and their relationship to body size. *Oecologia* **153**: 589–596

Fjerdingstad E.J. and Crozier R.H. 2006. The evolution of worker caste diversity in social insects. *Am. Nat.* **167**: 390–400

Hassrick J.L., Crocker D.E. and Costa D.P. 2013. Effects of maternal age and mass on foraging behavior and foraging success in the northern elephant seal. *Funct. Ecol.* **27**: 1055–1063

Hölldobler B. and Wilson E.O. 1990. *The Ants.* Cambridge, Massachusetts

Keiser C.N., Jones D.K., Modlmeier A.P. and Pruitt J.N. 2014. Exploring the effects of individual traits and within-colony variation on task differentiation and collective behavior in a desert social spider. *Behav. Ecol. Sociobiol.* **68**: 839–850

Jandt J. and Dornhaus A. 2009. Spatial organization and division of labor in the bumble bee, *Bombus impatiens*. *Anim. Behav*. **77**: 641–651

McNab B.K. 1963. Bioenergetics and the determination of home range size. *Am. Nat.* **97**: 133–140

Modlmeier A.P., Pamminger T., Foitzik S. and Scharf I. 2012. Cold resistance depends on acclimatization and behavioral caste in a temperate ant. *Naturwissenschaften* **99**: 811–819

Ness J.H., Bronstein J.L., Andersen A.N. and Holland J.N. 2004. Ant body size predicts dispersal distance of ant-adapted seeds: implications of small-ant invasions. *Ecology* **85**: 1244–1250

Okada Y., Plateaux L. and Peeters C. 2013. Morphological variability of intercastes in the ant *Temnothorax nylanderi*: pattern of trait expression and modularity. *Insect. Soc*. **60**: 319–328

Pie M.R. and Traniello F.A. 2007. Morphological evolution in a hyperdiverse clade: the ant genus *Pheidole*. *J. Zool*. **271**: 99–109

Pinter-Wollman N., Hubler J., Holley J.A., Franks N.R. and Dornhaus A. 2012. How is activity distributed among and within tasks in *Temnothorax* ants. *Behav. Ecol. Sociobiol.* **66**: 1407–1420

Roland J. and Taylor P.D. 1997. Insect parasitoid respond to forest structure at different spatial scales. *Nature* **386**: 710–713

Robinson E.J.H., Feinerman O. and Franks N.R. 2009. Flexible task allocation and the organization of works in ants. *Proc. R. Soc. B.* **276**: 4373–4380

Rueppell O. and Kirkma R.W. 2005. Extraordinary starvation resistance in *Temnothorax rugatulus* (Hymenoptera, Formicidae) colonies: Demography and adaptive behavior. *Insect. Soc.* **52**: 282–290

Schoener T. 1971. Theory of feeding strategies. *Annu. Rev. Ecol. Syst.* **2**: 369–404

Shutler D. and Mullie A. 1991. Size-related foraging behavior of the leaf-cutting ant *Atta colombica*. *Can. J. Zool.* **69**:1530–1533

Spaethe J. and Weidenmüller A. 2002. Size variation and forging rate in bumblebees (*Bombus terrestris*). *Insect. Soc.* **49**: 142–146

Tschinkel W.R., Mikheyev A.S. and Storz S.R. 2003. Allometry of workers of the fire ant, *Solenopsis invicta*. *J. Insect. Sci.* **3**: 3–11

Tschinkel W.R. 2013. The morphometry of *Solenopsis* fire ants. PloS one. 8: e79559

Wetterer J.K. 1999. The ecology and evolution of worker size-distribution in leaf-cutting ants (Hymenoptera: Formicidae). *Sociobiology* **34**: 119–144

Wilson E.O. 1980a. Caste and division of labor in leaf-cutter ants (Hymenoptera: Formicidae: *Atta*): I. The overall pattern in *A. sexdens*. *Behav. Ecol. Sociobiol.* **7**:143–146

Wilson E.O. 1980b. Caste and division of labor in leaf-cutter ants (Hymenoptera: Formicidae: *Atta*): II. The ergonomic optimization of leaf cutting. *Behav. Ecol. Sociobiol.* **7**: 157–165

Wilson E.O. 1984. The relationship between caste ratios and division of labor in the ant genus *Pheidole* (Hymenoptera: Formicidae). *Behav. Ecol. Sociobiol.* **16**: 89–98