HOKKAIDO UNIVERSITY

Title	Social-Organization Shift in the Sweat Bee, Lasioglossum baleicum (Hymenoptera, Halictidae), Corresponds to Changes in Foraging Activity of the Predatory Ant Tetramorium tsushimae (Hymenoptera, Formicidae)
Author(s)	Yagi, Norihiro; Hasegawa, Eisuke
Citation	Sociobiology, 58(1), 241-250
Issue Date	2011-01-01
Doc URL	http://hdl.handle.net/2115/66511
Type	article
File Information	39. Yagi+1 SocioBiol 11.pdf

Instructions for use

Social-Organization Shift in the Sweat Bee, *Lasioglossum baleicum* (Hymenoptera, Halictidae), Corresponds to Changes in Foraging Activity of the Predatory Ant *Tetramorium tsushimae* (Hymenoptera, Formicidae)

by

Norihiro Yagi* & Eisuke Hasegawa

ABSTRACT

Ecological factors, such as predation pressure or survival rate, affect social structure (e.g., gyny or founding modes) in social insects. Multiple females may cooperatively found a nest under severe ecological conditions. In bivoltine sweat-bees, most nests in the first reproductive period include a single female, but nest organization changes to cooperative in the second period. This fact predicts low predation pressures during the first period. However, few studies have examined corresponding changes between nest organization and predation pressures in social insects. Here, we compare the predation pressure between the two reproductive periods by using a sweat bee, *Lasioglossum baleicum*, that shifts the social organization from solitary to cooperative between the two reproductive periods. We recorded foraging activities of the predatory ant, *Tetramorium tsushimae*, during the whole reproductive season of *L. baleicum* and compared those between the first and second periods. The foraging activities of *T. tsushimae* were low in the first season but rapidly increased with the start of the second season. The foraging activities vary among bee populations depending on temperature conditions. The foraging activities were high during the cooperative period, suggesting that cooperation is a counter strategy to a high risk of predation. Further investigations on relationships between nest organization and strength of predation will bring us deeper insights into the effects of predators on the evolution of cooperation.

Key Words: Halictine bee, Sociality, Cooperation, Predation, Ants.

Laboratory of Animal Ecology, Department of Ecology and Systematics, Graduate School of Agriculture, Hokkaido University. Sapporo 060-8589, Japan.
*Corresponding Author: E-mail: vespa@res.agr.hokudai.ac.jp

INTRODUCTION

Evolutionary theory predicts that cooperation is adaptive under severe ecological conditions in which individuals cannot survive independently (Queller 1994). An important merit of cooperation is a high defensive efficiency to predators (Krams *et al*. 2010, Nowak *et al*. 2010). In fact, cooperative individuals seem to escape from attacks of predators (Queller 1989, Strassman & Queller 1989, Mappes *et al*. 1995, Smith *et al*. 2007, Krams *et al*. 2010, Yagi & Hasegawa 2011). Thus, predation pressure seems to affect the social organization of a colony.

Ecological factors such as predation risk and survivability affect social structures (e. g., founding mode or gyny) in social insects (Rissing *et al*. 1989; Queller 1994). In many species of annual social-insects, a single queen founds a nest and then shifts to a cooperative state after eclosing the first workers (Wilson 1971, Sakagami & Maeta 1986). In Halictine bees, a single female maintains a nest in the first reproductive period and then shifts to cooperative nest-organization in the following reproductive period(s) in the rest of the year (Sakagami & Hayashida 1968, Sakagami & Maeta 1986 Richards & Packer 1998, Miyanaga *et al*. 2000, Cronin & Hirata 2003, Wyman & Richards 2003). Thus, the risk of predation is likely to correspond with temporal changes in social organization in such species. However, no study has shown the corresponding change in both the predation risk and nest organization in the species that show a temporal shift in social organization.

The halictine bee *Lasioglossum baleicum* is a suitable subject for this topic because its nest organization shifts from solitary to cooperative between two reproductive periods within a year (Cronin & Hirata 2003, Hirata & Higashi 2008, Yagi & Hasegawa 2011). The second reproductive period can be discriminated distinctly from the first one since nests become inactive for approximately 30 days between the two periods (Cronin & Hirata 2003, Hirata & Higashi 2008). A main predator of *L. baleicum* seems to be an omnivorous ant, *Tetramorium tsushimae* (Yagi & Hasegawa 2011), and thus we can estimate risks of predation continuously by measuring foraging activities of this ant.

In this study, we measured foraging activities of *T. tsushimae* during the whole reproductive season of *L. baleicum* and investigated whether the foraging activity increased in the second reproductive period. The results will

indicate the relationship between the shift in social organizations and the risk of predation in *L. baleicum*.

MATERIALS & METHODS

Study organism and study sites

The halictine bee *Lasioglossum baleicum* is distributed throughout the Japanese archipelago (Murao & Tadauchi 2007). In Hokkaido (northern Japan), this species has two reproductive periods within a year; a single female maintains a nest in the first period (early May to early June) but multiple adult females cooperate to rear the second brood (early July to mid August) (Cronin & Hirata 2003, Hirata & Higashi 2008, Yagi & Hasegawa 2011). In the second period, several sterile daughters cooperate with a single fertile mother, indicating eusociality (Yagi & Hasegawa 2011). Many nests are found within a small area (ca. 2mx2), constituting a nest aggregation (Cronin & Hirata 2003, Hirata & Higashi 2008, Yagi & Hasegawa 2011).

We searched for nest aggregations of *L. baleicum* and found two sites, at the Field Science Center for Northern Biosphere, Hokkaido University Sapporo Experimental Forest (HU) and an experimental forest of Hokkaido Research Center Forestry and Forest Product Research Institute incorporated administrative agency (FL).

A main predator of *L. baleicum* seems to be an omnivorous ant, *Tetramorium tsushimae* (Yagi & Hasegawa 2011). Workers of this ant have been found in empty cells in *L. baleicum* nests (Yagi & Hasegawa 2011). In this ant genus, a scouting individual searches in soil crevices for food and recruits many nestmates when they find a large food source (Collingnon & Detrain 2010).

Measurements of ant foraging activity

We placed a piece of fish sausage (5mm thickness with 1cm diameter: OSA-KANA SOSAGE™, Seven-Eleven CO., LTD) on a piece of thin aluminum foil (5cm x 5cm). We set four such baits at equal intervals in a circle 5cm from from the peripheral edge of a nest aggregation. The baits were set at 1:00 pm. After an hour, recruited ants on a bait were collected and preserved in 70% Ethanol, and the number of ants on a bait was counted. When *T. tsushimae* workers on a bait were disturbed by other ants (e.g., *Camponotus japonicus*), we removed them since *C. japonicas* is not a predator of *L. baleicum*. We

measured the foraging activity of the ants once per 7-10 days during 29 May to 5 August in 2010 on sunny days. From June to July, the interval sometimes became larger than 10 days due to bad weather.

In addition to the measurements of the foraging activity, we also recorded the soil temperature of the center of the nest aggregations. The sensor of a digital thermometer (Multi Thermometer™, Japan pet drugs CO., LTD) was inserted into a depth of 1 cm from the ground surface at the center of each nest aggregation, and we recorded the soil temperature at both the start and the end of a measurement of the foraging activity. The average value of the two measurements was regarded as the soil temperature of that day. The measurements were conducted 10 times at HU and 9 times at FL.

Nest activity of *L. baleicum*

In order to know the end of the first reproductive period and the start of the second period, we observed foraging activities of adult bees, condition of the nest entrance (open or close) and discharge of soil from the nest entrance. From early June to early July, we checked the above activities at both the study sites on sunny days. The first reproductive period was judged to be over when none of the above activities was observed for three continuous days. The second reproductive period was regarded to start when any of the above activities was observed again after the end of the first period. In FL, the studied nest did not resume these activities, thus we assumed the second period of FL started with the same interval observed at HU.

Statistical analysis

In order to analyze factors affecting the foraging activity of the predatory ant, we constructed a multivariate model in which the number of workers recruited to bait was set as the response variable. We used the following explanatory variables: (1) number of days from the start of the investigation (DAY), (2) the soil temperature of each investigation (ST) and (3) the study sites (SITE). The numbers of recruited ants were overly dispersed to apply a generalized linear model (GLM), we used a generalized linear mixed model (GLMM) to correct the effect of this overdispersion. As DAY or SITE may affect ST, we evaluated the effects by using a GLM. We constructed a multivariate GLM model including DAY, SITE and the interaction term as explanatory variables.

For each analysis, we selected the best model by using a decreasing stepwise method based on Akaike's information criterion (AIC). Statistical significance of the regression coefficients of the best model was examined by a Wald test. All statistical analyses were conducted by the computer software "R" (ver. 2.9.2, R Development Core Team).

RESULTS

We found 19 and 1 nest(s) at HU and FL, respectively. The first reproductive period ceased in early June (5 June at HU; 8 June at FL: Fig. 1), and the second period started from late July (25 July at HU; 28 July at FL: Fig.1).

The GLMM for ant foraging selected a model that includes DAY and ST as explanatory variables (Table 1). Foraging activity of *T. tsushima*e continues to increase with both the DAY and ST but the activity was held low levels until the start of the second period (Fig. 1). The foraging activity increased rapidly with the start of the second period (Fig. 1). The foraging activities were significantly higher in the second reproductive period in both sites (for HU, $U=2.5$, $p=0.00033$, Mann-Whitney's U-test; for FL, $U=5.5$, $p=0.007$, Mann-Whitney's U-test).

The GLM analysis selected a model that includes only SITE as the explanatory variable (Table 2). The degree of regression coefficient of the SITE is statistically significant (Table 2).

Table 1. The results of model selection for generalized linear mixed model for the foraging activity of the ant, *Tetramorium tsushimae*. A model showing the lowest AIC is selected as the best model. Statistical tests were conducted only on the best model. DAY = Days from the start of the measurement: ST= Soil temperature of an investigation day: SITE = Study site.

Model	Residual deviance	AIC		Regression coefficient	Standard error	z value	p
DAY + ST + SITE	351.0	361.0					
DAY + ST	351.7	359.7	Intercept	-6.600	2.422	-2.725	0.006430
			DAY	0.09085	0.01390	6.535	0.00000000006360
			ST	0.2265	0.08838	2.563	0.01040
DAY	358.2	364.2					
ST	390.1	396.1					
SITE	398.4	404.4					

Table 2. The results of model selection for generalized linear model for the soil temperature of the investigation day at the study site. A model showing the lowest AIC is selected as the best model. Statistical tests were conducted only on the best model. DAY = Days from the start of the investigation; SITE = Study site (HU=0, FL=1).

Model	Residual deviance	AIC		Regression coefficient	Standard error	z value	p
DAY + SITE + interaction	149.8	103.2					
DAY + SITE	157.7	102.1					
DAY	207.1	105.3					
SITE	163.4	100.8	Intercept	28.26	0.9804	28.82	7.12×10^{-16}
			SITE	-3.301	1.424	-2.328	0.03320

DISCUSSION

The foraging activity of *T. tsushimae* was maintained at low levels during the first reproductive period but increased with the start of the second period (Fig. 1). Since the ST was positively correlated with the foraging activity (Fig. 1), it is suggested that low activity of the ants due to low ST resulted in low numbers of recruited workers in the first period.

The differences between the two periods are statistically significant in both the sites (see results section). In FL, because the nest did not resume its activity, we assumed the same interval between the two periods for this site. However, this assumption would not lead to an overestimation of the foraging activity in the second period in FL. Actual starting-day of the second period in FL would likely not be earlier than the estimated day since temperature is lower in FL than in HU, suggesting at least an equal or possibly longer interval in FL (see Hirata & Higashi 2008). In addition, the start of the second period has been subsequently confirmed in HU, and the difference between the two periods is statistically significant in HU. Thus, the foraging activity of *T. tsushimae* increased substantially in the second period.

Cooperative nest founding by multiple females found has been reported in sweat bees, wasps and ants (Sakagami & Hayashida 1968, Rissing *et al.* 1989, Sakagami *et al.* 1984, Queller & Strassman 1988, Strassman 1991, Shakarad & Gadagkar 1995, Richards & Packer 2000, Soucy 2002). Nesting by multiple females is regarded as a counter strategy to severe ecological conditions such as high predation risks and low nest survivability without cooperation (see Yagi & Hasegawa 2011). In a leaf-cutter ant, *Acromyrmex versicolor*, unrelated

females cooperatively found a nest, and such nests can produce more workers than solitary nests (Rissing *et al* 1989). A nest with many workers tends to win the survival battle among nests after eclosing of the first workers (Rissing *et al* 1989). In halictine bees, a high predation risk seems to induce nesting by multiple females in the first reproductive period (Soucy 2002). Under these conditions, cooperation by multiple adults would benefit all of the nest members. When such ecological constraints are absent, nesting by multiple females has evolutionary demerits for individuals, such as a low probability to become the final reproductive individual (Shakarad & Gadagkar 1995) and a low inclusive fitness even when cooperators were relatives (Gadagkar 1990). In such cases, solitary nest-founding would be selected for.

Lasioglossum baleicum nests are normally founded by a single female in the first period (Cronin and Hirata 2003). Low levels of ant foraging activities might result in a low risk of predation in the first period, leading to successful reproduction without coop-eration in this period. This study demonstrates a corresponding shift of social organization in *L. baleicum* in response to foraging activity of a predatory ant. The
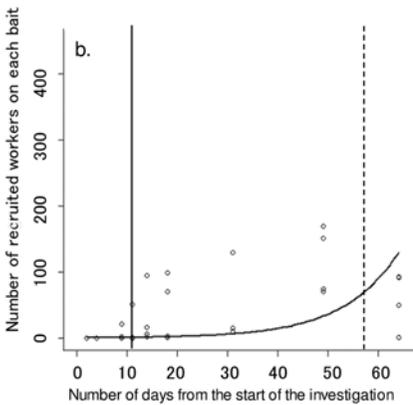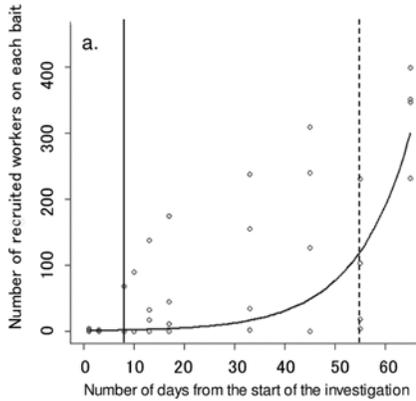

Fig. 1. Relationship between foraging activity of *Tetramorium tsushimae* and number of days from the start of the investigation in each study site. Fig. 1a and 1b show the results at HU and FL, respectively. Solid curves are estimated from the GLMM (see text) to which the soil temperature (ST) is fixed to the average soil temperatures during the investigation periods because DAY did not affect the ST in the GLM analysis (see text). Vertical solid lines show the day when the nest activity of the first reproductive period ceased. Vertical dotted lines show the day when the nest activity of the second reproductive period started.

direct determinant of both the changes is likely to be changes in soil temperature, but the bee may benefit from this correspondence. In *L. baleicum*, larval survival of cooperative nests in the second period has been improved drastically when compared with solitary nests (Yagi & Hasegawa 2011). Their results suggest that defensive efficiency of cooperative nests is higher than that of solitary nests. Therefore, the cooperation in the second period leads to high fitness by improving survival rate of larvae in this species.

The result of GLM suggest that the microclimate determines ST of each study site. Patterns of change in the soil temperature should vary among geographic areas. Thus, the strength and timing of change in predation pressure are predicted to vary among populations. In cold areas, low foraging activities of *T. tsushimae* due to low soil temperatures result in high rate of larval survival in solitary nests, leading to high fitness of a solitary nest compared with warm regions. Cooperative nests can rear large proportions of larvae despite strong predation pressure (see Yagi & Hasegawa 2011). This relationship predicts small difference in per capita fitness between a solitary founder and a cooperator in cold areas. On the other hand, the difference is predicted to become large in warm areas (see Yagi & Hasegawa 2011). Therefore, the proportion of solitary nests in a nest aggregation is predicted to vary among populations.

In halictine bees, social organization is highly plastic (Eickwort *et al.* 1996, Cronin & Hirata 2003, Hirata & Higashi 2008, Chapuisat 2010). A phylogenetic study showed frequent change in social organization from solitary to social and vise versa (Packer 1991). In addition, *L. baleicum* shows singular reproduction (= solitary state) in cold regions of Hokkaido (Cronin & Hirata 2002; Hirata & Higashi 2008). These fluctuations are likely to correlate with the strength of predation pressure on each species or population. *Lasioglossum baleicum* is known to distribute widely in Japan (Murase & Tadauchi 2007). As shown above, the number of reproductive periods and social organization vary among populations (Cronin & Hirata 2002; Hirata & Higashi 2008; Yagi & Hasegawa 2011). We require comparisons in several important ecological characters among populations, for example, proportions of solitary nests in a nest aggregation between reproductive periods. Further studies including such aspects will bring us many insights into effects of predation pressure on evolution of cooperation in this bee.

REFERENCES

Chapuisat, M. 2010. Evolution: Plastic sociality in a sweat bee. Current Biology 20(22): 977-979.

Collingnon, B. & C. Detrain 2010. Distributed leadership and adaptive decision-making in the ant *Tetramorium caespitum*. Proceeding of the Royal Society B Biological Science 277(1685): 1267-1273.

Cronin A.L. & M. Hirata 2003. Social polymorphism in the sweat bee *Lasioglossum* (*Evylaeus*) *baleicum* (Cockerell) (Hymenoptera, Halictidae) in Hokkaido, northern Japan. Insectes Sociaux 50(4): 379-386.

Eickwort, G.C., J.M. Eickwort, J.Gordon, M.A. Eickwort & W.T. Wcislo 1996. Solitary behavior in a high-altitude population of the social sweat bee *Halictus rubicundus* (Hymenoptera: Halictidae). Behavioral Ecology and Sociobiology 38(4): 227-233.

Gadagkar, R. 1990. Evolution of Eusociality: the advantage of assured fitness returns. Philosophical Transactions: Biological Sciences 329(1252): 17-25.

Hirata, M. & S. Higashi 2008. Degree-day accumulation controlling allopatric and sympatric variations in the sociality of sweat bees, *Lasioglossum* (*Evylaeus*) *baleicum* (Hymenoptera: Halictidae). Behavioral Ecology and Sociobiology 62(8): 1239-1247.

Krams, I., A. Bērziņš, T. Krama, D. Wheatcroft, K. Igaune & M.J. Rantala 2010. The increased risk of predation enhances cooperation. Proceeding of the Royal Society B Biological Science 277(1681): 513-518.

Mappes, J., A. Kaitala & R.V. Alatalo 1995. Joint brood guarding in parent bugs: -An experiment on defence against predation. Behavioral Ecology and Sociobiology 36: 343-347.

Miyanaga, R., Y. Maeta & K. Hoshikawa 2000. Nesting biology and Occurrence of social nests in a bivoltine and basically solitary halictine bee, *Lasioglossum (Lasioglossum) scitulum* Smith (Hymenoptera: Halictidae). Entomological Science 3(2): 291-302.

Murao, R. & O. Tadauchi 2007. A revision of the Subgenus *Evylaeus* of the genus *Lasioglossum* in Japan (Hymenoptera, Halictidae) Part I. ESAKIA 47: 169-254.

Nowak, M.A., C.E. Tarnita & E.O. Wilson 2010. The evolution of eusociality. Nature 466: 1057-1062.

Packer, L. 1991. The evolution of social behavior and nest architecture in sweat bees of the subgenus *Evylaeus* (Hymenoptera: Halictidae): a phylogenetic approach. Behavioral Ecology and Sociobiolgy 29(3): 153-160.

Queller, D.C. 1989. The evolution of eusociality: reproductive head starts of workers. Proceedings of the National Academy of Sciences of the United States of America 86(9): 3224–3226.

Queller, D.C. 1994. Extended parental care and the origin of eusociality. Proceeding of the Royal Society B Biological Science 256(1346): 105–111.

Queller, D.C. & J.E. Strassman 1988. Reproductive success and group nesting in the paper wasp, *Polistes annularis*. *In:* Clutton-Block, T.H. (ed.). Reproductive success: studies of individual variation in contrasting breeding systems. University of Chicago Press, Chicago, United States of America: 76-96.

Richards, M.H. & L. Packer 1998. Demography and relatedness in multiple-foundress nests of the social sweat bee, *Halictus ligatus*. Insectes Sociaux 45(1): 97-109.

Rissing, S.W., G.B. Pollock, M.R. Higgins, R.H. Hagan, & D.R. Smith 1989. Foraging specialization without relatedness or dominance among co-founding ant queens. Nature 338: 420-422.

Sakagami, S.F. & K. Hayashida 1968. Bionomics and sociology of the summer matrifilial phase in the social halictine bee, *Lasioglossum duplex*. Journal of the Faculty of Science Hokkaido University Series V I. Zoology 16(3): 413-513.

Sakagami, S.F. & Y. Maeta 1986. From Loneliness to Unequalness: The Life of the Small Carpenter Bees and their Allies. Tokai University Press, Tokyo, Japan: 9-36.

Shakarad, M. & R. Gadagkar 1995. Colony founding in the primitively eusocial wasp, *Ropalidia marginata* (Hymenoptera: Vespidae). Ecological Entomology 20(3): 273-282.

Smith, A.R., W.T. Wcislo & S. O'Donnell 2007. Survival and productivity benefits to social nesting in the sweat bee *Megalopta genalis* (Hymenoptera: Halictidae). Behavioral Ecology and Sociobiolgy 61(7): 1111-1120.

Soucy, S.L. 2002. Nesting biology and socially polymorphic behavior of the sweat bee *Halictus rubicundus* (Hymenoptera: Halictidae). Annals of the Entomological Society of America 95: 57-65.

Strassmann, J.E. 1991. Costs and benefits of colony aggregation in the social wasp, *Polistes annularis*. Behavioral Ecology 2(3): 204-209.

Wilson, E.O. 1971. Insect Societies. The Belknap Press of Harvard University, Cambridge, Massachusetts, United States of America: 548.

Wyman, L.M. & M.H. Richards 2003. Colony social organization of *Lasioglossum malachurum* Kirby (Hymenoptera, Halictidae) in southern Greece. Insectes Sociaux 50(3): 201-211.

Yagi, N. & E. Hasegawa 2011. Both cooperation and nest position improve larval survival in the sweat bee, *Lasioglossum (Evylaeus) baleicum*. Journal of Ethology 29(1): 63-67.