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## RESEARCH ARTICLE - ANTS

### Effects of environmental factors on life cycle regulation in *Lasius japonicus* Santschi (Formicidae)

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#### Abstract

This study investigated environmental factors that regulate oviposition by queens and colony development in *Lasius japonicus* Santschi. Newly mated queens were collected from fields in Okayama, Japan. The insects were maintained outdoors or under a long- or short-day photoperiod at 30 °C, 25 °C, 20 °C, or 15 ± 1 °C. All queens died within 50 days at 30 °C, whereas all or most of the queens survived at lower temperatures. At 25 °C, many pupae were observed approximately 1 month after the onset of oviposition. Diapause in either queens or workers was not induced at 25 °C. At 20 °C, many larvae did not pupate, indicating that larval diapause was induced. At 15 °C, hatching was not recorded and eggs disappeared. Low temperatures may induce reproductive diapause in queens. There were no significant differences between long-day (LD 16:8 h) and short-day (LD 12:12 h) conditions at any temperature. Under outdoor conditions, when summer temperature was moderate in 2005, queens started their nuptial flights in June, and pupation was recorded three times. However, when summer temperature was high in 2006, pupation occurred 1–2 times before winter, with queens making their nuptial flights as late as mid-July. Eggs and pupae disappeared in most colonies before the arrival of winter. Only queens, adult workers, and larvae were observed during winter. The present study showed that queens of *L. japonicus* founded and developed their colonies for as long as environmental conditions remained favorable, by responding to changes in temperature.

#### Introduction

In the temperate region, insects commonly undergo winter diapause. Even when environmental conditions are suitable for growth and reproduction, insects anticipate the occurrence of unfavorable conditions and enter diapause by responding to specific environmental stimuli, such as short day length or low temperature (Lees, 1955; Danilevsky, 1961; Tauber et al., 1986; Danks, 1987; Košťál, 2006). In warm temperate regions or at higher latitudes, ants enter winter diapause according to the criteria delineated by Kipyatkov (2001). In relatively warm climates, low temperature is the primary environmental stimulus for the induction of diapause, although day length is critical for many other insect orders (Kipyatkov, 1993, 2001). Ants inhabiting higher latitudes often enter diapause after a certain period of reproduction and development, regardless of environmental stimuli, and even

when they were kept under stable warm conditions in the laboratory (Kipyatkov, 1993, 2001).

Workers have been shown to influence the regulation of diapause in queens or larvae. For instance, larvae tend to emerge as workers without entering diapause if they are reared by workers that have been exposed to low temperatures. In contrast, larvae tend to enter diapause if they are reared by workers that have passed the winter or experienced low temperature in the laboratory (e.g., Brian, 1955; Weir, 1959; Kipyatkov et al., 1996, 1997; Kipyatkov & Lopatina, 1999).

Reproductive workers of the Japanese queenless ant, *Pristomyrmex pungens*, lay eggs during the long-day photoperiod, whereas they enter diapause in response to the short-day photoperiod (Muramatsu & Numata, 2002). In contrast, the second to fifth instar larvae of *Amblyopone silvestrii* Wheeler are found year-round, but the eggs, first instar larvae, pupae, and callow adults are mainly found in



summer (Masuko, 2003a). For example, cocoons were found from July to October, with the greatest numbers occurring in August (Masuko, 2003a). However, detailed experimental studies on the seasonal adaptations of Japanese ants have not been conducted in other species.

Claustral colony founding is common in many ant species. This strategy involves a newly mated queen starting a colony without any help from workers by using nutrient reserves (Hölldobler & Wilson, 1990). After the workers emerge, the development of the colony is highly dependent on the social conditions of the nest, such as the size and structure of the population and the age of workers (e.g., Brian, 1953, 1957a, 1957b; Schneirla, 1957; Tschinkel, 1988; Børgesen & Jensen, 1995; Masuko, 2003b). Although social effects influence the development of a colony, such effects might also hinder direct investigations of how environmental factors affect the physiological status of queens.

*Lasius japonicus* Santschi is found in the Japan islands, Korean peninsula, and Taiwan (JADG, 2003). It was previously assumed to be *Lasius niger* (Linnaeus), which is widely distributed in the Palearctic region, but was formally identified as *L. japonicus* by Seifert (1992). Oviposition of *L. niger* queens collected from Russia is not affected by photoperiod, but is strongly controlled by temperature. The queens stop ovipositing soon after being transferred to a temperature of 20 °C or less (Kipyatkov, 2001). Induction and termination of diapause are partly affected by the physiological state of workers. Specifically, workers in the spring physiological state influence larval diapause when exposed to low temperatures (Kipyatkov et al., 1996). Furthermore, as in other ants found at high latitudes, diapause induction is obligatory at the colony level. Specifically, colony development ceases within a certain period after the onset of oviposition by queens, even at optimal temperatures (Kipyatkov, 2001). These seasonal regulations of queen oviposition and colony development are adaptive for high latitudinal regions, where the seasons that are favorable for growth and reproduction are short. However, in southwestern Japan, the climate is moderate; thus, insects are able to develop and reproduce for a longer period. Therefore, we hypothesized that *L. japonicus* has evolved physiological adaptations to the warm climate, and will exhibit more intensive colony development than *L. niger*. In the present study, we collected *L. japonicus* Santschi queens immediately after their nuptial flight, and maintained them under various photoperiod and temperature combinations to determine the effect of environmental factors on colony founding. The results of this study are expected to provide novel insights about the life cycle adaptations of this species under warm temperate climate.

## Materials and methods

Within 3 hours of their nuptial flight, more than 300 queens of *L. japonicus* were collected from Okayama City (34.7°N, 133.9°E), Japan, between late June and early August

in 2005 and 2006. Queens that shed their wings were separately reared in plastic cases (70 × 40 mm, 20 mm in depth). The bottom of the cases was covered by plaster, and water was provided ad libitum. The insects were maintained outdoors or under a long- or short-day photoperiod at 30 °C, 25 °C, 20 °C, or 15 ± 1 °C. We used a long-day light:dark (LD) photoperiod of 16:8 h, which is slightly longer than the day length at the summer solstice in Okayama, and is also the length often used to examine the life cycle of insects in southwestern Japan (e.g., Musolin & Numata, 2003; Shintani & Numata, 2010). A short-day photoperiod of LD 12:12 h was also used. This photoperiod was equivalent to the day length slightly after the autumnal equinox, including the twilight portion of the day. Because *L. japonicus* exhibits claustral colony founding, food was not provided until the first worker, or minim, emerged as an adult. After the workers emerged, dried bloodworm and artificial diet for adult beetles (Fujikon Co. Ltd., Nose, Osaka, Japan) were supplied as food twice a week.

In this study, 21 queens were reared individually in 21 cases for each experimental condition (168 queens in total). Mortality and oviposition of queens were recorded daily until day 100 and 180 at 25 °C and 20 °C, respectively. We recorded the pre-oviposition period and the daily number of pupae to assess colony development in this study. Because eggs and small larvae were attached together by queens, we did not record the number of them. In addition, we did not record the number of fast-moving workers. Experiments in the laboratory were discontinued at day 100 and 180 at 25 °C and 20 °C, respectively, which was when counting the number of pupae became too difficult. Queens at 15 °C were transferred to either a long- or short-day photoperiod at 25 °C at 100 days after collection, when they were considered to be in diapause. After the transfer to 25 °C, queens were kept another 100 days, at which point the experiments were discontinued.

Some queens were reared under natural conditions. Specifically, plastic cases were placed in cages that could not be reached by direct sunlight on the campus of Okayama University of Science. The daily average temperature data recorded at the meteorological station closest to the university (about 3 km south of the university) was obtained from the Japan Meteorological Association (<http://www.data.jma.go.jp/obd/stats/etrn/index.php>). In February 2006, 5 queens maintained under outdoor conditions were dissected to determine whether they were in diapause, by assessing the development of ovarioles under a stereoscopic microscope.

## Results

All queens died without producing workers when reared at 30 °C under LD 16:8 h. The median longevity was 33 days (range, 23–45). However, at lower temperatures, queens survived for 100 days, both under LD 16:8 h and 12:12 h (Table 1). At 25 °C, 5 queens died within a few days after collection under the long-day photoperiod.

**Table 1.** Effects of temperature and photoperiod on queen survival and colony development in *Lasius japonicus*.

Temperature	Photoperiod	Initial number of colonies	Percentage of queen survival at day 100	Average ( $\pm$ S.D.) pre-oviposition period (days)	Average ( $\pm$ S.D.) pre-pupal period (days)
25 °C	LD 16:8 h	21	47.6	3.4 $\pm$ 1.5 (16)	25.0 $\pm$ 1.0 (10)
	LD 12:12 h	21	100	3.3 $\pm$ 1.0 (21)	24.0 $\pm$ 2.0 (21)
20 °C	LD 16:8 h	21	95.2	5.3 $\pm$ 4.0 (21)	48.9 $\pm$ 11.9 (19)
	LD 12:12 h	21	100	5.0 $\pm$ 3.6 (21)	49.3 $\pm$ 13.8 (17)
15 °C	LD 16:8 h	21	85.7	5.0 $\pm$ 1.6 (21)	-
	LD 12:12 h	21	100	5.8 $\pm$ 3.6 (21)	-

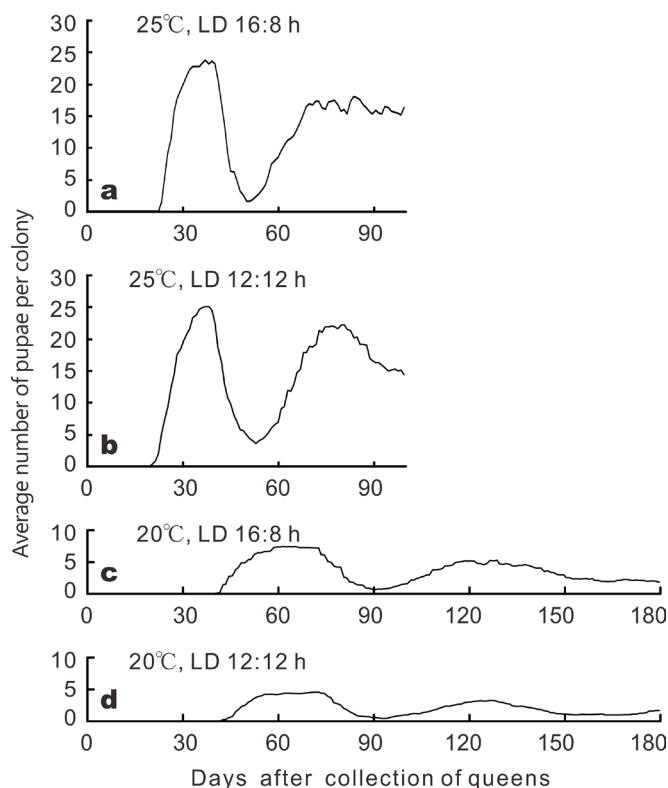
Number of queens starting to oviposit is shown in parentheses after the average pre-oviposition period. Number of colonies in which pupae emerged is shown in parentheses after the average pre-pupal period.

However, all the other 16 queens started laying eggs about 3 days after collection. Under LD 12:12 h, all 21 queens started laying eggs soon after collection. Also at 20 and 15 °C, all queens started oviposition under any experimental conditions, indicating that they have mature eggs at nuptial flight. Under the long-day photoperiod, 6 queens which had started oviposition died before the emergence of pupae, whereas no queen died under the short-day photoperiod. Pupation was recorded approximately 25 days after the beginning the experiment at 25 °C (Table 1, Fig 1a, b). There was no significant difference in the average pre-pupation period (from the collection of queens to the appearance of pupae) between long- and short-day conditions ( $p > 0.05$ ,  $t$ -test). Average numbers of pupae

increased sharply, and peaked at about day 40. Average number ( $\pm$  S.D.) of pupae was  $23.2 \pm 2.0$  ( $N = 10$ ) and  $22.5 \pm 7.5$  ( $N = 21$ ) on day 40 under LD 16:8 h and 12:12 h, respectively. There was no significant difference in the number of pupae between long- and short-day conditions ( $p > 0.05$ ,  $t$ -test). Subsequently, the number of pupae decreased and adult workers emerged. When workers of the first batch started emerging, many pupae and a few well-grown larvae, but not small larvae, were found in the colonies. Second pupation initiated at around day 50, and the number of pupae increased until approximately day 80. The second peak in pupation was less clear than the first peak, because of less synchronization among colonies.

At 20 °C, queens started laying eggs approximately 5 days after collection (Table 1). There was no significant difference in the pre-oviposition period between the 2 photoperiods ( $p > 0.05$ ,  $t$ -test). Eggs hatched at about 30 days after the collection of queens. Although all queens, except one under LD 16:8 h, survived 180 days, pupae did not emerge in 1 and 4 colonies under LD 16:8 h and LD 12:12 h, respectively. Pupation started at about 50 days after the collection of queens. There was no significant difference in the average pre-pupation period between long- and short-day conditions ( $p > 0.05$ ,  $t$ -test). Pupation peaks were observed twice on days 40-80 and days 100-150, regardless of the photoperiod (Fig 2c, d). At day 60, the average number ( $\pm$  S.D.) of pupae was  $7.3 \pm 7.9$  ( $N = 19$ ) and  $4.2 \pm 4.0$  ( $N = 17$ ) days under LD 16:8 h and 12:12 h, respectively. There was no significant difference in the average number of pupae at day 60 between the 2 photoperiods ( $p > 0.05$ ,  $t$ -test). In addition, larvae of different instars were always present until the end of the experimental period, even though their sizes and numbers were not recorded.

At 15 °C, all queens started oviposition under both LD 16:8 h and 12:12 h, respectively, but hatching was not observed. Thereafter, the eggs disappeared until day 100, even though most queens were still alive (Table 1). Because no dead or rotted eggs were found in the container, it was assumed that they had been eaten by the queens. The queens resumed egg laying 8.5-9.2 days on average after being transferred to 25 °C at day 100 (Table 2). There was no significant difference in the period from the transfer to the resumption of oviposition



**Fig 1.** Effects of photoperiod and temperature on the mean number of *Lasius japonicus* pupae.  $N = 16-21$ .

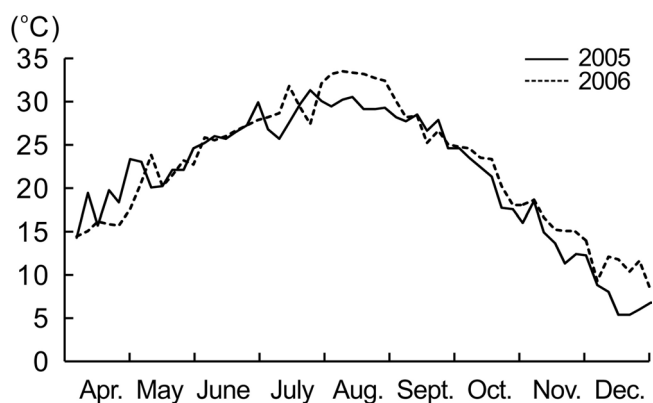
**Table 2.** Effects of photoperiod on colony development after temperature rising in *Lasius japonicus*.

Rearing conditions before transfer	Rearing conditions after transfer	Initial number of colonies	Average ( $\pm$ S.D.) pre-oviposition period (days)	Average ( $\pm$ S.D.) pre-pupal period (days)
15 °C, LD 16:8 h	25 °C, LD 16:8 h	9	9.0 (9)	34.7 $\pm$ 5.8 (3)
	25 °C, LD 12:12 h	9	9.2 $\pm$ 0.7 (9)	29.8 $\pm$ 8.3 (8)
15 °C, LD 12:12 h	25 °C, LD 16:8 h	11	8.5 $\pm$ 1.5 (11)	36.9 $\pm$ 4.1 (7)
	25 °C, LD 12:12 h	10	9.6 $\pm$ 1.0 (10)	31.6 $\pm$ 6.1 (8)

Number of queens starting to oviposit is shown in parentheses after the average pre-oviposition period. Number of colonies in which pupae emerged is shown in parentheses after the average pre-pupal period.

among experimental treatments (two-way ANOVA,  $p > 0.05$ ; Table 3). Larvae hatched from these eggs. Although some queens died after the transfer to 25 °C, pupation was observed in 3-8 colonies. The periods from the transfer of queens to the onset of pupation were 29.8-36.9 days in the 4 experimental treatments, which was 5-12 days longer than the periods for colonies transferred directly from the field to 25 °C (see Table. 1).

Under natural conditions, the rearing experiment was started in late June, 2005. Summer temperatures were not very high, with a monthly average of 25.8 °C and 26.7 °C in July and August, respectively (Fig 2). All 21 queens laid eggs soon after collection, and pupation initiated in late July (Fig 3).

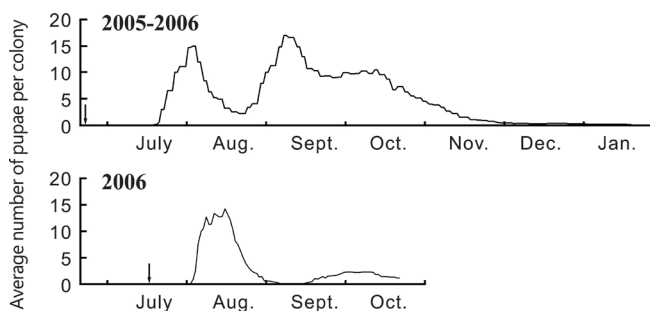
**Fig 2.** Change in 5-day mean temperature under quasi natural conditions from April to December in 2005 and 2006 (Japan Meteorological Agency, 2015).

The greatest number of first-brood pupae occurred in early August. Second- and third-brood larvae pupated in September and October, respectively. Approximately half of the colonies had produced 3 broods by the end of the growing season, while the remaining colonies produced 2 broods. The number of pupae in the second brood was similar to that in the first, but was higher than that in the third brood. The third pupation peak was unclear in the figure because of less synchronization among colonies. In winter, the pupae disappeared in most colonies. The queens, workers, and the larvae of several instars were found in the colonies. In the end of January 2006

**Table 3.** Summary of two-way ANOVA testing for the effects of photoperiods before and after transfer from 15 to 25 °C on the pre-oviposition period in *Lasius japonicus*.

Source of variation	Sum of squares	d.f.	MS	F	P
Photoperiod before transfer	75.383	1	75.38	1.817	0.191
Photoperiod after transfer	63.965	1	63.97	1.541	0.228
Interaction	18.334	1	18.33	0.442	0.513
Error	912.899	22	41.50		

when rearing experiment was discontinued, 19 of 21 queens were still alive. Some of them were dissected in February, but no mature eggs were found in the ovaries. In 2006, when spring temperature was less than that in 2005 (see Fig 2), the nuptial flight started in mid-July. However, the 2006 summer temperatures were higher (about 2-3 °C difference) than those of 2005. Four queens died within a few days of the collection, and 17 queens started oviposition under outdoor conditions. Pupation of the first-brood larvae occurred in August (Fig 3). However, in September or later, considerably fewer pupae were produced in 2006 compared to 2005, with no production of second-brood pupae occurring in approximately half of the colonies in 2006.

**Fig 3.** Mean number of *Lasius japonicus* pupae under quasi-natural conditions. Arrows indicate the timing of the nuptial flight of queens. N = 21 in 2005 and 17 in 2006.

## Discussion

Queen mortality and colony development of *L. japonicus* were highly dependent on temperature. All queens died without producing workers at 30 °C. Yet, during summer, the daily mean temperature often exceeds 30 °C in Okayama (Japan Meteorological Agency, 2015). Thus, *L. japonicus* nests are usually constructed underground (JADG, 2003), where changes in temperature are more moderate than those on the ground surface. However, a solitary queen may not construct a nest deep underground soon after mating. The broods of *Solenopsis invicta* Buren develop faster in sunny, warmer sites; yet, total production and queen survival are lower at sunny sites compared to shady sites (Tschinkel, 1993). Our results confirm the importance of environmental temperature during colony foundation.

At 25 °C, the number of pupae noticeably increased at 30–40 days after oviposition (Fig 1a, b). Synchronized pupation indicates that *L. japonicus* larvae from Okayama do not undergo diapause at this temperature. Moderate temperature is considered to be suitable for colony development. The number of pupae decreased once, but increased again on days 60–70, approximately 30 days after the pupation of the first brood. The interval between the 2 successive pupation peaks indicates that queens started laying the eggs of the second brood when pupation of the first brood had initiated. Similar cyclic egg-laying is also exhibited in other ant species, such as *Myrmica rubra* Linnaeus (Brian, 1951, 1957b), *Eciton hamatum* Fabricius, and *Eciton burchelli* Westwood (Schneirla, 1957). The reproductive activity of queens in the army ants, *E. hamatum* and *E. burchelli*, is highly dependent on the cycle of colony development. Specifically, when larvae reach maturity, workers feed both the larvae and the queen, which results in cyclic ovarian maturation (Schneirla, 1957). In the present study, second oviposition began before the emergence of workers. Therefore, in *L. japonicus*, egg-laying of the second brood may initiate without feeding by workers. In *A. silvestrii*, oophagy by the first- and second-instar larvae results in cyclic egg production. In this species, the number of eggs increases when the larvae molt into the third instar (Masuko, 2003b). Although we found egg cannibalism in *L. japonicus*, its impact on the egg population has not been evaluated. Further studies might be necessary to elucidate the mechanism of cyclic oviposition.

The number of *L. japonicus* pupae at 20 °C was considerably lower than that at 25 °C (Fig 2c, d). Furthermore, different instar larvae were always present in most of the colonies throughout the experiments. The suppression of pupation indicates that many larvae were in diapause. Among warm temperate ant species, larval diapause is often induced by low temperature (Kipyatkov, 2001). Our results indicate that *L. japonicus* larval diapause is regulated by temperature, as in other ant species.

At 15 °C, eggs disappeared from the colony without hatching, although most of the queens survived for 100 days of the experimental period (Fig 1). Thus, this temperature

might be too low to allow the completion of regular embryonic development. The queens needed a certain period of time to resume oviposition after they were transferred from 15 °C to 25 °C. Both the pre-oviposition and pre-pupation periods were longer than those in colonies where queens were directly transferred from the field to constant 25 °C. This delay indicates that ovarian development was arrested at 15 °C. Furthermore, queens that were reared outdoors had no mature eggs in their ovaries during winter. These results indicate that low temperatures induce queens to enter reproductive diapause. In *L. niger* from Russia, colony development is known to be suppressed by low temperatures. In this species, queens stop ovipositing and enter diapause soon after they are transferred to 20 °C or 17 °C under both long- and short-day photoperiods (Kipyatkov, 1993). However, *L. japonicus* colonies continuously developed during the 180 days of experiments at 20 °C, indicating that the queens of this species are less sensitive to low temperature than those of *L. niger*. Therefore, *L. japonicus* has become adapted to the warm climate of Okayama, because queens are able to develop the colony for a longer period.

In many ants of temperate regions, photoperiod does not influence the induction of diapause, even though it is the most important environmental stimulus in many other insect orders (Kipyatkov, 1993, 2001). The queens and larvae of *L. niger* from Russia do not show a photoperiodic response for the induction of diapause (Kipyatkov, 1993). Our findings confirm that photoperiod has a limited effect on the induction of diapause, even in *L. japonicus*.

In some ant species, larvae and queens that were reared by workers without exposure to low temperature tended to enter diapause (e.g., Brian, 1955; Weir, 1959; Kipyatkov et al., 1996, 1997; Kipyatkov & Lopatina, 1999). In the present study, worker of the first brood emerged in the experimental treatments at 25 °C and 20 °C. However, there was no clear difference in the number of pupae between the first and second broods (Fig 1). Even though the average number of pupae tended to be greater in the first brood compared to the second brood, this difference was considered to be due to the less synchronization among colonies. Thus, workers do not induce diapause in worker larvae and queens, even if they are not exposed to low temperatures. This phenomenon is considered to be an adaptation to warmer climate, in which more than 1 brood may be produced.

These responses to environmental factors provide a reasonable explanation for the seasonal development of colonies under natural conditions. Queens make the nuptial flight in early summer when the temperature rises to around 25 °C, which is suitable for the rapid development of colonies (Fig 2). In 2005, as many as 3 broods were produced before the end of the growing season (Fig 3). Temperatures in July and August of 2005 were lower and more suitable than those of the following year, allowing the development of second and third broods. In comparison, in 2006, queens produced broods

once or twice when the nuptial flight occurred in mid-July or later. In August, the number of second-brood pupae was small under high summer temperatures of approximately 30 °C. This near-lethal temperature may suppress the development of colonies. Similarly, environmental temperature has been shown to markedly affect colony founding by *S. invicta* (Tschinkel, 1993). In our study, the number of pupae decreased after mid-October, and almost none were found in the winter of both years, indicating that larval diapause is induced by low temperatures.

The present study showed that *L. japonicus* is well adapted to the warm temperate climate of Okayama. Queens founded and developed their colonies for as long as environmental conditions remained favorable, by responding to changes in temperature.

## References

- Børgesen, L.W. & Jensen, P.V. (1995). Influence of larvae and workers on egg production of queens of the pharaoh's ant, *Monomorium pharaonis* (L.). *Insectes Sociaux*, 42: 103-112. doi: 10.1007/BF01245702.
- Brian, M.V. (1951). Summer population changes in colonies of the ant *Myrmica*. *Physiologia Comparata et Oecologia*, 2: 248-262.
- Brian, M.V. (1953). Brood rearing in relation to worker number in the ant *Myrmica*. *Physiological Zoology*, 26: 355-366.
- Brian, M.V. (1955). Studies of caste differentiation in *Myrmica rubra* L. 3. larval dormancy, winter size and vernalisation. *Insectes Sociaux*, 2: 85-114. doi: 10.1007/BF02224096.
- Brian, M.V. (1957a). The growth and development of colonies of the ant *Myrmica*. *Insectes Sociaux*, 4: 177-190. doi: 10.1007/BF02222152.
- Brian, M.V. (1957b). Serial organization of brood in *Myrmica*. *Insectes Sociaux*, 4: 191-210. doi: 10.1007/BF02222153.
- Danilevsky, A.S. (1961). [Hidaka T and Masaki S Japanese translation, 1966] Photoperiodism and Seasonal Development of Insects. Tokyo: University of Tokyo Press, 293p.
- Danks, H.V. (1987). Insect dormancy: An Ecological Perspective. Ottawa: Biological Survey of Canada, 439p.
- Hölldobler, B. & Wilson, E.O. (1990). The Ants. Cambridge: Harvard University Press, 732p.
- Japanese Ant Database Group (JADG). (2003). Super visual Encyclopedia. Ants of Japan. Tokyo: Gakken, 196p (in Japanese).
- Japan Meteorological Agency. (2015). Table of the monthly means and monthly total. <http://www.data.jma.go.jp/obd/stats/etrn/index.php>. (accessed date: 1 March, 2015).
- Kipyatkov, V.E. (1993). Annual cycles of development in ants: Diversity, evolution, regulation. *Proceedings of the Colloquia on Social Insects*, 2: 25-48.
- Kipyatkov, V.E. (2001). Seasonal life cycles and the forms of dormancy in ants (Hymenoptera: Formicoidea). *Acta Societatis Zoologicae Bohemicae*, 65: 211-238.
- Kipyatkov, V.E., Lopatina, E.B. & Pinegin, A.Yu. (1996). Influence of the queen and worker ants on onset and termination of the larval diapause in *Lasius niger* (L.) (Hymenoptera, Formicidae). *Entomological Review*, 76: 514-520.
- Kipyatkov, V.E., Lopatina, E.B. & Pinegin, A. Yu. (1997). Social regulation of development and diapause in the ant *Leptothorax acervorum* (Hymenoptera: Formicidae). *Entomological Review*, 77: 248-255.
- Kipyatkov, V.E. & Lopatina, E.B. (1999) Social regulation of larval diapause by workers of three species of the ant genus *Myrmica* Latreille (Hymenoptera, Formicidae). *Entomological Review*, 77: 1138-1144.
- Košťál, V. (2006). Eco-physiological phases of insect diapause. *Journal of Insect Physiology*, 52: 113-127. doi: 10.1016/j.jinsphys.2005.09.008.
- Lees, A.D. (1955). *The Physiology of Diapause in Arthropods*. Cambridge: Cambridge University Press, 151p
- Masuko, K. (2003a). Analysis of brood development in the ant *Amblyopone silvestrii*, with special reference to colony bionomics. *Entomological Science*, 6: 237-245. doi: 10.1046/j.1343-8786.2003.00028.x.
- Masuko, K. (2003b). Larval oophagy in the ant *Amblyopone silvestrii* (Hymenoptera, Formicidae). *Insectes Sociaux*, 50: 317-322. doi: 10.1007/s00040-003-0688-y.
- Muramatsu, N. & Numata, H. (2002). Seasonal changes in ovarian development and its control by photoperiod in the Japanese queenless ant, *Pristomyrmex pungens*. *Proceedings XIV International Congress of IUSI* (p. 205). Hokkaido University.
- Musolin, D.L. & Numata, H. (2003). Photoperiodic and temperature control of diapause induction and colour change in the southern green stink bug *Nezara viridula*. *Physiological Entomology*, 28: 65-74. doi: 10.1046/j.1365-3032.2003.00307.x.
- Schneirla, T.C. (1957). Theoretical consideration of cyclic processes in Doryline Ants. *Proc. Am. Phil. Soc.* 101: 106-133.
- Seifert, B. (1992). A taxonomic revision of the palaearctic members of the ant subgenus *Lasius* s. str. (Hymenoptera: Formicidae). *Abhandlungen und Berichte des Naturkundemuseums Görlitz*, 66: 1-67.
- Shintani, Y. & Numata, H. (2010) Adaptive significance of the recurrent photoperiodic response in a spring-breeding carabid beetle, *Carabus yaconinus*. *Entomological Science*, 13: 367-374. doi: 10.1111/j.1479-8298.2010.00403.x.

Tauber, M.J., Tauber, C.A. & Masaki, S. (1986). Seasonal Adaptations of Insects. New York: Oxford University Press, 426p.

Tschinkel, W.R. (1988). Social control of egg-laying rate in queens of the fire ant, *Solenopsis invicta*. Physiological Entomology, 13: 327-350. doi: 10.1111/j.1365-3032.1988.tb00484.x.

Tschinkel, W.R. (1993). Resource allocation, brood production and cannibalism during colony founding in the fire ant, *Solenopsis invicta*. Behavioral Ecology and Sociobiology, 33: 209-223. doi: 10.1007/BF02027118.

Weir, J.S. (1959). The influence of worker age on trophogenic larval dormancy in the ant *Myrmica*. Insectes Sociaux, 6: 271-290. doi: 10.1007/BF02224411.

