Emergence at lower temperatures facilitates movement of the flesh flies *Parasarcophaga similis* and *Boettcherisca peregrina* (Diptera: Sarcophagidae) into temperate and subarctic regions

Atsuko Moribayashi¹, Hiromu Kurahashi¹ and DeMar Taylor* ²

* Corresponding author: taylor.de.mar.ge@u.tsukuba.ac.jp

¹ Department of Medical Entomology, National Institute of Infectious Diseases,
1–23–1 Toyama, Shinjuku-ku, Tokyo 162–8640, Japan

² Faculty of Life and Environmental Sciences, University of Tsukuba,
1–1–1 Tennodai, Tsukuba, Ibaraki 305–8572, Japan

(Received: 28 January 2021; Accepted: 11 August 2021)

Abstract: Differences in rates of diapause induction are thought to produce differences in the distribution of flies. Therefore, we investigated differences in the day length for entering diapause and effective chill treatment for termination of pupal diapause in *Parasarcophaga similis* and *Boettcherisca peregrina* flies found in Japan. Results showed maximum rates of diapause incidence for *P. similis* colonies from Sapporo, Tokyo and Nagasaki were 98% under 13L : 11D at 20°C, 100% under 11L : 13D and 80% under 10L : 14D, respectively. Diapause incidences for *B. peregrina* colonies from Tokyo and Nagasaki were 100% and 98% under 13L : 11D at 20°C. Emergence rates for diapausing pupae of *P. similis* (Sapporo) chilled at 4°C then transferred to diapause-terminating conditions at 27°C (16L : 8D) or 20°C (11L : 13D) were 65% and 80%. In *B. peregrina* (Tokyo), chill treatment was effective for 89% emergence. Adult *P. similis* (Sapporo) flies emerging from pupae that experienced chill treatment laid larvae that entered diapause at an incidence of 99.5%, whereas adult *B. peregrina* (Tokyo) laid 22% larvae destined for diapause. These flesh flies appear to move into new environments by successfully developing the ability to emerge at lower temperatures and possibly avoiding the maternal effect.

Key words: diapause, chill treatment, emergence, maternal effect, distribution

Introduction

Flesh flies are forensically very important flies that feed on carrion, dung or decaying material and are distributed from tropical to subarctic regions of the world (Saigusa et al., 2005; Cherix et al., 2012; Ren et al., 2017; Wang et al., 2017). In addition, they are potential vectors of myiasis with reports of human cases caused by *Parasarcophaga similis* and *Boettcherisca peregrina* in Japan (Chigusa et al., 1994; Hatsushika et al., 2002; Miura et al., 2005). The scientific names of these flies follow the “Catalogue of the Insects of Japan”, which was edited by the Editorial Committee of the Catalogue of the Insects of Japan, and published in 2014 by the Entomological Society of Japan, Touka Shodo, Fukuoka, Japan. These scientific names are considered to be standard before and after Pape’s catalogue (1996). Traditional classification and combinations of generic and specific scientific names are adopted in the part on Sarcophagid flies of the “Catalogue of the Insects of Japan”.

Diapause has allowed these flies to expand their distributions. A latitudinal gradient in the critical day length for diapause induction suggests that there is a corresponding gradient in selection for diapause or non-diapause in the Sarcophagidae (Kurahashi and Kano, 1984; Kano et al., 1967; Moribayashi et al., 2001, 2008). Photoperiod appears to be the main environmental cue for organisms to prepare for seasonal changes (Nelson et al., 2010). Species expanding into higher latitudes experience a change in the photoperiod and must then adjust to the new environmental conditions by modifying their behavior and physiology (Bradshaw and Holzapfel, 2007). Successful expansion into a new environment requires subsequent evolutionary changes critical for the new photoperiod (Gaston, 2003; Bradshaw and Holzapfel, 2007; Urbanski et al., 2012).

In Japan, flesh flies are distributed widely from temperate Kyushu to subarctic Hokkaido. The flesh flies *P. similis* and *B. peregrina* enter diapause at the pupal stage to withstand the harsh conditions of winter. *Parasarcophaga similis* is widely distributed in the northern areas of Eurasia from Japan to England (Pape, 1996). On the other hand, *B. peregrina* is widely distributed in tropical and temperate regions from
Mauritius and the Seychelles across Asia, Oceania and Northern Australia (Kurahashi and Ohtaki, 1979; Kurahashi and Kano, 1984; Pape, 1996; Moribayashi et al., 2001). *Parasarcophaga similis* and *B. peregrina* enter pupal diapause in the temperate and subarctic zones initiated by a short photoperiod perceived during embryonic and early larval development under low temperatures (Denlinger, 1971, 1974; Saunders, 1971; Vinogradova, 1976; Kurahashi and Ohtaki, 1979; Henrich and Denlinger, 1982; Gnagny and Denlinger, 1984; Moribayashi et al., 2001, 2002, 2008; Tanaka et al., 2008; Goto, 2009; Tagaya et al., 2010).

In a previous study, we examined the effects of chill treatment on diapause termination of *B. peregrina* collected from Tokyo, BP-Tokyo colony (Moribayashi et al., 1999). Diapausing pupae of *B. peregrina* experiencing periods of 4°C for three months showed effective diapause termination in approximately 90% of the diapausing pupae. Based on these observations, we concluded that chill treatment is an important factor affecting diapause termination in these flies. Acquisition of pupal diapause by flesh flies appears to allow them to spread north into the temperate and subarctic zones (Moribayashi et al., 2001). Therefore, in the present study we investigated differences in the day length for entering diapause and effective chill treatment for termination of pupal diapause of three geographically different colonies of *P. similis* and two colonies of *B. peregrina*. Furthermore, we examined the diapause incidence of next generation larvae raised from diapause terminated adult flies of the Ps-Sapporo colony and Bp-Tokyo colony to see whether these flies may show a maternal effect. From these results we clarify differences leading to the temperate distribution of *B. peregrina* and subarctic distribution of *P. similis*.

**Materials and Methods**

**Experimental animals**

Three colonies of *P. similis* referred to as Ps-Nagasaki, Ps-Tokyo and Ps-Sapporo were collected from the southern temperate (Nagasaki City 32.78°N and 129.86°E), middle temperate (Tokyo, 35.72°N and 139.81°E) and northern subarctic areas (Kita-Hiroshima City, 42.98°N and 141.57°E) of Japan. Two colonies of *B. peregrina* referred to as Bp-Tokyo and Bp-Nagasaki were also collected from the same locations in Tokyo and Nagasaki. *Boettcherisca peregrina* could not be collected from Sapporo despite several attempts. Origins of all colonies were a single wild female collected from the field of each area. Laboratory colonies were established through serial cultures under controlled environmental conditions for continued development (16L:8D, 60–80% RH, 27°C). Larvae were fed pork liver and water, whereas adults were supplied fresh liver and sugar. These strains were maintained routinely and their population sizes never dropped below an estimated 100 individuals. Approximately 150 newly emerged adults were transferred to short day (SD) conditions (11L:13D) at 20°C and larvae from the adults used for experiments to determine diapause incidence and suitable chill treatment.

**Critical photoperiod of diapause incidence**

Larvae of each colony born under SD at 20°C were grown to mature larvae under the same conditions as above. Water immersion treatment of mature larvae inhibits pupariation and subsequent transfer to dry conditions induces larvae to simultaneously pupariate (Ohtaki, 1966; Moribayashi et al., 2002). Mature larvae were treated with water immersion for at least two days and then separated into groups for eight photophases; 9, 10, 11, 12, 13, 14, 15 and 16 hrs of light per day. Subsequently, approximately 100 mature larvae from each photophase were transferred to small cups (10 cm diameter) with dry sawdust for pupariation. After three weeks the anterior tips of the pupae were opened to determine the developmental status. Flies with no sign of adult development were determined as diapausing pupae, whereas those developing adult head structures were counted as non-diapausing pupae (Fraenkel and Hsiao, 1968).

**Diapausing pupae and chill treatment**

Diapausing pupae of Ps-Sapporo and Bp-Tokyo were prepared for use in experiments to determine the effects of chilling on diapause. To induce diapause, larvae were obtained from females held under SD at 20°C and the adult flies laid larvae destined for diapause. The larvae entered pupal diapause and the pupae were kept for at least 2 months under the same conditions. These diapausing pupae were divided into groups of 40–50 individuals and stored in containers of dry sawdust. The diapausing pupae were transferred to 4°C for 0 to 35 weeks and then transferred for diapause termination to 27°C under long day (LD) or 20°C under SD. The rate of adult emergence was examined for effects of different chilling times and temperatures on diapause termination.

**Larvae from adults destined for diapause**

After twenty-eight weeks in Bp-Tokyo and twelve weeks in Ps-Sapporo, chilled diapausing pupae were transferred to 20°C under SD for diapause termination and diapause incidence of larvae laid by diapause experienced adults examined by opening the anterior tips to determine developmental status as described above.

**Statistical Analysis**

Significant differences in incidences of diapause at all daylengths in which diapause occurred for Ps-Nagasaki, Ps-Tokyo and Ps-Sapporo were determined using Bonferroni pairwise test after Kurskal–Wallis
test. Significant differences between Bp-Nagasaki and Bp-Tokyo were analyzed with Welch’s t-test. Chi-square test was used to determine the significance of differences in the laying of diapause larvae between Ps-Sapporo and Bp-Tokyo. All statistical analyses were performed with R version 4.0.

Results

Critical photoperiod and day lengths for diapause incidence

Figure 1A shows the photoperiodic response curves for three colonies of *P. similis* collected from Sapporo (Ps-Sapporo), Tokyo (Ps-Tokyo) and Nagasaki (Ps-Nagasaki) under each day length condition at 20°C. The maximum diapause incidences for the three colonies at 20°C were 98% under 13L:11D, 99% under 11L:13D and 85% under 10L:14D, respectively. The day lengths for 50% diapause incidence were 13 h 40 min in Ps-Sapporo, 12 h 30 min in Ps-Tokyo and 11 h 30 min in Ps-Nagasaki with significant differences between the critical day lengths of approximately 1 h (*p* < 0.05). Figure 1B shows the photoperiodic response curves of two *B. peregrina* colonies from Tokyo (Bp-Tokyo) and Nagasaki (Bp-Nagasaki) under each day length at 20°C. The maximum incidences of diapause were 100% in Bp-Tokyo under 13L:11D and 98% in Bp-Nagasaki under 13L:11D, whereas the 50% critical day lengths were 13 h 50 min and 13 h 30 min, respectively, with significant but much smaller differences between the two colonies (*p* < 0.05).

Effect of chill treatment on adult emergence

The effects of chill treatment on diapause termination are shown in Figures 2 and 3. Adult emergence after chill treatment at 4°C for Ps-Sapporo occurred a minimum of 9 days after exposure to 27°C in diapause experienced pupae chilled for 13, 17, 21 and 26 weeks (Fig. 2A). Pupae with a short chilling period (0, 1 and 2 weeks) required more than 15 days at 27°C for adults to emerge (Fig. 2A). On the other hand, the earliest emergence for Bp-Tokyo flies during the 9 day interval occurred after a shorter length of chill treatment (8, 10, 12 and 15 weeks) (Fig. 2B). The minimal interval of days needed for adult emergence of Bp-Tokyo and Ps-Sapporo was also 9 days (Fig. 2A, 2B). The most effective chilling periods for adult emergence were 13, 17, 21 and 26 weeks for Ps-Sapporo and 8, 10, 12 and 15 weeks for Bp-Tokyo (Fig. 2A, 2B). For adult emergence from diapause in Ps-Sapporo 5 weeks longer chilling was needed when compared to Bp-Tokyo.

Figure 3A and 3B show adult emergence rates after

---

**Fig. 1.** Diapause incidence (%) of colonies of *P. similis* (A) and *B. peregrina* (B). Three colonies of *P. similis* were collected from Sapporo City of Northern Japan, Tokyo Metropolis of Central Japan and Nagasaki City of Southern Japan (A). Two colonies of *B. peregrina* were collected from Tokyo and Nagasaki (B). The horizontal axis shows day length (L: light hours, D: dark hours in one day). The vertical axis shows percent of diapause incidence at each day length. Dashed lines indicate the 50% diapause incidences and 50% critical day lengths. Kruskal–Wallis test for multiple comparison showed *p*<0.05 significance, and pairwise test with Bonferroni for daylengths 14L10D through 9L15D (A). Welch t-test showed *p*<0.01 in daylengths 14L10D through 9L15D and *p*<0.05 for 15L9D (B). For further details refer to the Material and Methods.
chilling periods in Ps-Sapporo at 27°C and 20°C and Bp-Tokyo at 27°C. The highest incidence of emergence of Ps-Sapporo for the length of chilling was 17 weeks at 4°C and the emergence rate with diapause termination was 65% (Fig. 3A). The rate of adult emergence for diapause termination with transfer to 20°C increased to more than 80% after 23 and 28 weeks of chill treatment, showing that 20°C is better than 27°C for diapause termination in *P. similis* (Fig. 3A). Conversely, diapause termination was higher at 27°C for *B. peregrina*. Adult emergence in Bp-Tokyo was highest with chill treatment for 12 weeks and 89% adult emergence was observed (Fig. 3B). A difference of 5 weeks in periods of chilling needed to stimulate adult emergence coincide well with the natural differences in the length of the cold seasons of Sapporo (subarctic zone) and Tokyo (temperate zone), indicating each species has adapted to a chilling period necessary for survival in their respective environments.
Larvae destined for diapause produced by diapause experienced females

Pupae of Ps-Sapporo exposed to 4°C for 23 weeks emerged at a rate of 89% after transfer to 20°C at SD and laid larvae 14 days and 18 days after adult emergence. Two hundred and forty four larvae were laid after 14 days and 243 after 18 days kept under SD. Table 1 shows the rate of diapause incidence in these larvae. The percentages of larvae that entered pupal diapause were 99.6% and 99.5%, essentially all Ps-Sapporo larviposited under the subarctic conditions became larvae destined for diapause.

On the other hand adults of B. peregrina, Bp-Tokyo, experiencing pupal diapause laid larvae under SD, larvae laid from those adults entered pupal diapause a rate of 22, 23 and 22% in 3 separate experiments (Table 1). The pupal diapause rate in Bp-Tokyo is significantly lower than the 99% diapause rate for Ps-Sapporo (p<0.01). These results show that B. peregrina, originally a tropical species, can also develop diapause leading to the subarctic distribution of P. similis these flies in the world (Pape, 1996). Parasarcophaga similis flies are concentrated from temperate subarctic to frigid zones in the northern hemisphere (Pape, 1996), whereas B. peregrina flies are concentrated in both the northern and southern hemispheres around the equator (Kurahashi and Kano, 1984; Kano et al., 1967). Both species belong to the family Sarcophagidae and strongly resemble each other but have different distributions. Rates of diapause for B. peregrina collected in the tropical zone are absent or extremely low, but high in specimens collected from high latitudes (Kurahashi and Ohtaki, 1989; Moribayashi et al., 2001). Since B. peregrina occurs in the tropical and temperate zones where temperatures are relatively high, a longer low-temperature period during its diapause period likely adversely affects its survival. In this study, a low temperature (5°C) period of 12 weeks increased the rate of eclosion but further continuation of the low-temperature period decreased this rate in the Bp-Tokyo colony. Figure 4A and B show the changes in day length (A) and temperatures (B) during the year 2000 in Sapporo City, Metropolitan Tokyo and Nagasaki City (NINS, 2000). The day length and temperature coincide well with changes where the colony was collected in Tokyo, the winter season is 3–4 months from December to March (Moribayashi et al., 1999). In the case of P. similis, the eclosion rate increased when low-temperature conditions continued 17 or more weeks. This period matches the temperatures where the colony was collected in Sapporo, winter season is 5–6 months from November to April.

The present study also showed differences in the rates of adult emergence at different temperatures and lengths of chill treatment. To stimulate adult emergence of Ps-Sapporo a temperature of 20°C was better than 27°C (Fig. 3A). However, for adult emergence of Bp-Tokyo the highest rate of emergence occurred at 27°C in this study (Fig. 3B) and 27°C in a previous study by Moribayashi et al. (1999). Numerous attempts to collect B. peregrina from Sapporo were in vain despite a previous record that flies were collected in Sapporo (Kurahashi and Kano, 1984; Kano et al.,

### Table 1. Diapause incidence (%) in larvae larviposited from adults that experienced diapause under short day conditions.

| No. of larvae used | Emerging adults | Diapausing pupae | Diapause incidence (%) | Average (%) |
|--------------------|-----------------|------------------|------------------------|-------------|
| P. similis, Ps (Sapporo) | 244 | 1 | 243 | 99.6 |
| 201 | 1 | 200 | 99.5 |
| B. peregrina, Bp (Tokyo) | 100 | 78 | 22 | 22 |
| 100 | 77 | 23 | 23 |
| 100 | 78 | 22 | 22 |

*Adult flies used in this experiment experienced pupal diapause and laid larvae under short day conditions at 20°C.*

**p<0.01 Pearson’s Chi-squared test with Yates continuity correction.

Discussion

The purpose of the present study was to compare the importance of day lengths for entering diapause and effective chill treatments for termination of pupal diapause leading to the subarctic distribution of P. similis, Ps-Sapporo and temperate distribution of B. peregrina, Bp-Tokyo using controlled laboratory experiments. Furthermore, the diapause incidence of next generation larvae laid from diapause terminated adult flies were examined to consider whether there is a maternal effect in these two species.

The photoperiods that induced diapause in 50% of P. similis showed approximately one hour differences between Sapporo and Tokyo as well as between Tokyo and Nagasaki. The photoperiods for the B. peregrina populations were similar in both Tokyo and Nagasaki. While P. similis in Sapporo entered diapause under a LD of 13L, the flies in Nagasaki entered diapause under a SD of 11L, indicating the flies have adapted to the day length changes in the temperate and subarctic zones. In contrast, the colonies of B. peregrina, a species that originated in the tropical zone, did not show significant differences in day length conditions in the temperate zones.

Differences in rates of diapause induction are thought to produce differences in the distribution of these flies in the world (Pape, 1996). Parasarcophaga similis flies are concentrated from temperate subarctic to frigid zones in the northern hemisphere, whereas B. peregrina flies are concentrated in both the northern and southern hemispheres around the equator (Kurahashi and Kano, 1984; Kano et al., 1967). Both species belong to the family Sarcophagidae and strongly resemble each other but have different distributions. Rates of diapause for B. peregrina collected in the tropical zone are absent or extremely low, but high in specimens collected from high latitudes (Kurahashi and Ohtaki, 1989; Moribayashi et al., 2001). Since B. peregrina occurs in the tropical and temperate zones where temperatures are relatively high, a longer low-temperature period during its diapause period likely adversely affects its survival. In this study, a low temperature (5°C) period of 12 weeks increased the rate of eclosion but further continuation of the low-temperature period decreased this rate in the Bp-Tokyo colony. Figure 4A and B show the changes in day length (A) and temperatures (B) during the year 2000 in Sapporo City, Metropolitan Tokyo and Nagasaki City (NINS, 2000). The day length and temperature coincide well with changes where the colony was collected in Tokyo, the winter season is 3–4 months from December to March (Moribayashi et al., 1999). In the case of P. similis, the eclosion rate increased when low-temperature conditions continued 17 or more weeks. This period matches the temperatures where the colony was collected in Sapporo, winter season is 5–6 months from November to April.

The present study also showed differences in the rates of adult emergence at different temperatures and lengths of chill treatment. To stimulate adult emergence of Ps-Sapporo a temperature of 20°C was better than 27°C (Fig. 3A). However, for adult emergence of Bp-Tokyo the highest rate of emergence occurred at 27°C in this study (Fig. 3B) and 27°C in a previous study by Moribayashi et al. (1999). Numerous attempts to collect B. peregrina from Sapporo were in vain despite a previous record that flies were collected in Sapporo (Kurahashi and Kano, 1984; Kano et al.,
In Sapporo, the temperatures remain very low from November through April so a B. peregrina, Bp-Sapporo, colony would most likely not be able to go through eclosion.

In contrast, P. similis was easily collected from Sapporo in large numbers. When the temperature for adult emergence after chill treatment was 27°C, the rate of P. similis adult emergence was 65% after 17 weeks. However, when the temperature was 20°C, the emergence rate increased to more than 80% after 18 weeks of chill treatment. This adult emergence of over 80% continued up to 28 weeks, which is greater than half a year. Therefore, the best length of exposure to low temperatures for the Sapporo colony of P. similis exceeds 17 weeks at 20°C. Parasarcophaga similis is known to be widely distributed in the Eurasian continent including the main islands of Japan (Pape, 1996), but have never been recorded from the Ryukyu Islands (Kano et al., 1967). Although several investigations were attempted to find and create a colony originating from the Okinawa-Honto and adjacent islands by the second author (HK), we were unsuccessful in collecting P. similis from these Ryukyu Islands including the main islands of Japan (Pape, 1996), but have never been recorded from the Ryukyu Islands (Kano et al., 1967). Although several investigations were attempted to find and create a colony originating from the Okinawa-Honto and adjacent islands by the second author (HK), we were unsuccessful in collecting P. similis from these Ryukyu Islands belonging to the Oriental Zoogeographical Region. This indicates P. similis are only distributed in the temperate and subarctic zones of Japan. The ability of P. similis to emerge at lower temperatures may have allowed this species to move into the subarctic regions.

Generally, Sarcophaga flies that experience diapause do not lay larvae destined for diapause because of a maternal effect (Fraenkel and Hsiao, 1968; Denlinger, 1971; Saunders, 1971; Vinogradova, 1976; Henrich and Denlinger, 1982; Gnagey and Denlinger, 1984; Rockey et al., 1989). The progeny from some species of mother flesh flies experiencing pupal diapause do not enter diapause even when they are reared in an environment suitable to induce diapause (Denlinger, 1985). Namely, the effect is transmitted solely by the female parent and the capacity for pupal diapause can be restored in the progeny of the next generation only by rearing a generation under long days.

Although the results are preliminary and need further experimental confirmation, the present study showed that Ps-Sapporo females and Bp-Tokyo females that experienced diapause were able to lay larvae destined for pupal diapause. The rate of diapause incidence of larvae from Ps-Sapporo females was approximately 100%, whereas from Bp-Tokyo was 22%. Moribayashi et al. (2002) showed in an earlier study the same results for B. peregrina with approximately 20 to 24% of larvae laid by diapause experienced females being destined for diapause. This was true whether the adult females came from larvae that had experienced water immersion or not. Larval-pupal pupariation can be inhibited by keeping larvae under conditions of water immersion (Ohtaki and Takahashi, 1972). This inhibition happens because ecdysone release from the ring glands of mature larvae is blocked. However, after the larvae are transferred to dry conditions, further development resumes and the arrested larvae metamorphose into pupae (Moribayashi et al., 1992). Boettcherisca peregrina larvae destined for non-diapause converted to larvae destined for diapause with water immersion treatment under short days (diapause induction), but larvae destined for diapause converted to larvae destined
for non-diapause with water immersion treatment under long days (diapause breaking) (Moribayashi et al., 2002). This strongly suggests the larvae themselves possess factors to determine whether they enter diapause or non-diapause and shows that sensitivity to short day information is higher in the early larval stage. McMatters and Saunders (1996) and Cymborowski et al. (1996) showed through crosses between northern and southern strains of the blow fly Calliphora vicina that the incidence of diapause reflects the genetic background of the mother alone, but diapause duration is a larval phenomenon influenced by genes inherited from both parents. As we showed in this study, both P. similis females from the subarctic zone and B. peregrina from the temperate zone have the ability to lay larvae destined for pupal diapause. Therefore, maternal effects appear to play important roles in the regulation of diapause but the responses vary among species and strains, and other factors such as photoperiod and temperatures of microenvironments may alter the physiology responses allowing flies to adapt to temperate and subarctic conditions.

Embryos and early stage larvae of B. peregrina and P. similis appear to possess a high sensitivity to photoperiodic information and this has allowed them to move into temperate and arctic zones by developing a photoperiod sensitive diapause mechanism. The emergence of P. similis distributed in the subarctic regions decreases with high temperatures and under SD conditions with chilling. Therefore, diapause termination cannot proceed in areas that lack seasonal periods of low temperatures. However, after a long diapause adult flies that experience exposure to low temperatures can lay larvae that quickly enter diapause if bad weather occurs. This is very important for the survival of these flies in the subarctic zones and allows them to complete a life cycle in one year and lay diapause larvae that can survive the harsh subarctic winters. Similar mechanisms may have functioned in B. peregrina to allow this species to expand its distribution from tropical areas into temperate areas. Lehmann et al. (2014) showed that behavioral plasticity in burrowing of Leptinotarsa decemlineata, an invasive Colorado potato beetle, may have facilitated the synchronization of burrowing behavior with physiological traits so as to allow Northward expansion of their range. Similarly, plasticity in the physiology and behavior of these flesh flies may have facilitated their movements into temperate and subarctic areas. More extensive studies on flesh flies are needed to better clarify the mechanisms that regulate diapause and allow the range expansion of these forensically important flies.

Acknowledgements

We thank Yoshio Tsuda and Mutsuo Kobayashi, Department of Medical Entomology, National Institute of Infectious Diseases, for their valuable suggestions and helpful advice.

References

Bradshaw, W. E. and Holzapfel, C. M. 2007. Evolution of animal photoperiodism. Annu. Rev. Ecol. Evol. Syst., 38: 1–25.
Cherix, D., Wyss, C. and Pape, T. 2012. Occurrences of flesh flies (Diptera: Sarcophagidae) on human cadavers in Switzerland, and their importance as forensic indicators. Forensic Sci. Int., 220: 158–163.
Chigusa, Y., Tanaka, K., Yokoi, H., Matsuda, H., Sasaki, Y., Ikadatsu, Y. and Baba, K. 1994. Two cases of otomyiasis caused by Sarcophaga peregrina and S. similis (Diptera: Sarcophagidae). Jpn. J. Sanit. Zool., 45: 153–157.
Cymborowski, B., Hong, S. F., McMatters, H. G. and Saunders, D. S. 1996. S-antigen antibody partially blocks entrainment and the effects of constant light on the circadian rhythm of locomotor activity in the adult blow fly, Calliphora vicina. J. Biol. Rhythms, 11: 68–74.
Denlinger, D. L. 1971. Embryonic determination of pupal diapause in the flesh fly, Sarcophaga crassipalpis. J. Insect Physiol., 17: 1815–1822.
Denlinger, D. L. 1974. Diapause potential in tropical flesh flies. Nature, 252: 223–224.
Denlinger, D. L. 1985. Hormonal Control of Diapause, In: Comprehensive Insect Physiology, Biochemistry and Pharmacology, Vol. 8. (eds. Kerkut, G. A. and Gilbert, L. I.), pp. 353–412, Pergamon Press, Oxford, England.
Fraenkel, G. and Hsiao, C. 1968. Manifestations of a pupal diapause in two species of flies, Sarcophaga argyrostoma and S. bullata. J. Insect Physiol., 14: 689–705.
Gaston, K. 2003. The structure and dynamics of geographic ranges. Oxford Series in Ecology and Evolution. 259 pp., Oxford University Press, New York.
Gnagey, A. L. and Denlinger, D. L. 1984. Photoperiodic induction of pupal diapause in the flesh fly, Sarcophaga crassipalpis: embryonic sensitivity. J. Comp. Physiol. B, 154: 91–96.
Goto, S. G. 2009. Genetic analysis of diapause capability and association between larval and pupal photoperiodic responses in the flesh fly, Sarcophaga similis. Physiol. Entomol., 34: 46–51.
Hatsushika, R., Ushirogawa, H. and Iwanaga, Y. 2002. A case study of human otomyiasis caused by Parasarcophaga similis (Meade, 1876) (Diptera:Sarcophagidae) found in Hiroshima, Japan. Kawasaki Med., 28: 33–41.
Henrich, V. C. and Denlinger, D. L. 1982. A maternal effect that eliminates pupal diapause in progeny of the flesh fly, Sarcophaga bullata. J. Insect Physiol., 28: 881–884.
Kano, R., Field, G. and Shionaga, S. 1967. Sarcophagidae (Insecta, Diptera). Fauna Japonica, 7: 1–168.
Kurahashi, H. and Ohtaki, T. 1979. Induction of pupal diapause and photoperiodic sensitivity during early development of Sarcophaga peregrina larvae. Jpn. J. Med. Sci. Biol., 32: 77–82.
Kurahashi, H. and Kano, R. 1984. Phylogeny and geographical distribution of the genus Boettcherisca Rohdendorf (Diptera: Sarcophagidae). Jpn. J. Med. Sci. Biol., 37: 27–34.
Kurahashi, H. and Ohtaki, T. 1989. Geographic variation in the incidence of pupal diapause in Asian and Oceanian species of the flesh fly, Boettcherisca (Diptera: Sarcophagidae). Physiol. Entomol., 14: 291–298.
Lehmann, P., Lytyninen, A., Piironen, S. and Lindstrom, L. 2014. Northward range expansion requires synchronization of both overwintering behavior and physiology with photoperiod in the invasive Colorado potato beetle (Leptinotarsa decemlineata). Oecologia, 176: 57–68.
McMatters, H. G. and Saunders, D. S. 1996. The influence of each
parent and geographic origin on larval diapause in the blow fly, Calliphora vicina. J. Insect Physiol., 42: 721–726.

Miura, M., Hayasaka, S., Yamada, T., Hayasaka, Y. and Kamimura, K. 2005. Ophthalmomyiasis caused by larvae of Boettcherisca peregrina. Jpn. J. Ophthalmol., 49: 177–179.

Moribayashi, A., Kurahashi, H. and Ohtaki, T. 1992. Physiological differentiation of the ring glands in mature larvae of the flies fly, Boettcherisca peregrina, programmed for diapause or non-diapause. J. Insect Physiol., 38: 177–183.

Moribayashi, A., Wells, J. D. and Kurahashi, H. 1999. Chilling period for effective survival of diapausing pupae of the flesh fly, Boettcherisca peregrina, collected from Tokyo. Med. Entomol. Zool., 50: 129–133.

Moribayashi, A., Shudo, C. and Kurahashi, H. 2001. Latitudinal variation in the incidence of pupal diapause in Asian and Oceanian populations of the flesh fly, Boettcherisca peregrina (Diptera: Sarcophagidae). Med. Entomol. Zool., 52: 263–268.

Moribayashi, A., Hiraoka, T., Kurahashi, H. and Agui, N. 2002. Pupal diapause induction in larvae destined for non-diapause of the flesh fly, Boettcherisca peregrina (Diptera: Sarcophagidae). Med. Entomol. Zool., 53: 279–288.

Moribayashi, A., Hayashi, T., Taylor, D., Kurahashi, H. and Kobayashi, M. 2008. Different responses to photoperiod in non-diapausing colonies of the flesh fly, Boettcherisca peregrina. Physiol. Entomol., 33: 31–36.

Nelson, R. J., Denlinger, D. L. and Somers, D. E. 2010. Photoperiodism, the biological calendar. 580 pp., Oxford University Press, Oxford.

NINS (National Institute of Natural Sciences). 2000. Natural Astronomical Observatory of Japan Annual Science Report. 86 pp. Maruzen Publishing Co. Ltd., Tokyo, Japan.

Ohtaki, T. 1966. On the delayed pupation of the fleshfly, Sarcophaga peregrina Robineau-Desvoidy. Jpn. J. Med. Sci. Biol., 19: 97–104.

Ohtaki, T. and Takahashi, M. 1972. Induction and termination of pupal diapause in relation to the change of ecdysone titer in the fleshfly, Sarcophaga peregrina. Jpn. J. Med. Sci. Biol., 25: 369–376.

Pape, T. 1996. Catalogue of the Sarcophagidae of the World (Insecta: Diptera). Mem. Entomol. Int., 8: 1–558.

Ren, L. P., Deng, H. X., Dong, S. Z., Li, J. B., Hu, X. H., Cai, J. F. and Guo, Y. D. 2017. Survey of indoor sarcosaphagous insects. Trop. Biomed., 34: 284–294.

Rockey, S. J., Miller, B. B. and Denlinger, D. L. 1989. A diapause maternal effect in the flesh fly, Sarcophaga bullata: Transfer of information from mother to progeny. J. Insect Physiol., 35: 553–558.

Saigusa, K., Takamiya, M. and Aoki, Y. 2005. Species identification of the forensically important flies in Iwater prefecture, Japan based on mitochondrial cytochrome oxidase gene subunit I (COI) sequences. Leg. Med. (Tokyo), 7: 175–178.

Saunders, D. S. 1971. The temperature-compensated photoperiodic clock programming” development and pupal diapause in the fleshfly, Sarcophaga argyrostoma. J. Insect Physiol., 17: 801–812.

Tagaya, J., Numata, H. and Goto, S. G. 2010. Sexual difference in the photoperiodic induction of pupal diapause in the flesh fly Sarcophaga similis. Entomol. Sci., 13: 311–319.

Tanaka, M., Tachibana, S. I. and Numata, H. 2008. Sensitive stages for photoperiodic induction of pupal diapause in the flesh fly Sarcophaga similis (Meade) (Diptera: Sarcophagidae). Appl. Entomol. Zool., 43: 403–407.

Urbanski, J., Mogi, M., O’Donnell, D., DeCotiis, M., Toma, T. and Armbruster, P. 2012. Rapid adaptive evolution of photoperiodic response during invasion and range expansion across a climatic gradient. Am. Nat., 179: 490–500.

Vinogradova, E. B. 1976. Embryonic photoperiodic sensitivity in two species of fleshflies, Parasarcophaga similis and Boettcherisca septentrionalis. J. Insect Physiol., 22: 819–822.

Wang, Y., Wang, J. F., Zhang, Y. N., Tao, L. Y. and Wang, M. 2017. Forensically important Boettcherisca peregrina (Diptera: Sarcophagidae) in China: Development pattern and significance for estimating postmortem interval. J. Med. Entomol., 54: 1491–1497.