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Source: Zoological Science, 28(12) : 875-881

Published By: Zoological Society of Japan

URL: <https://doi.org/10.2108/zsj.28.875>

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A Cicada That Ensures Its Fitness during Climate Warming by Synchronizing Its Hatching Time with the Rainy Season

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A shift in phenology due to climate change is associated with some recent changes in populations, as it can disrupt the synchrony between organisms' requirements and resource availability. This conceptual framework has been developed mostly in systems of trophic interactions. Many coincidental changes, however, are involved in trophic interactions, preventing us from describing the direct impact of phenological shifts on fitness consequences. Here we address the phenological relationship in a simple non-trophic interaction to document a causal process of a warming-driven fitness change in a cicada, *Cryptotympana facialis*, whose numbers increased dramatically in Osaka, Japan in the late 20th century. We show that synchrony of the rainy season and hatching time may have a substantial influence on hatching success, by 1) shifting the time of completion of embryonic development, and 2) supplying water at various intervals. We estimate the change in hatching time over the last eleven decades (1901–2009) based on meteorological records and the temperature-dependent rate of *C. facialis* embryogenesis. Our estimate shows that hatching had initially occurred after the rainy season, and that warming had advanced it into the rainy season in the late 20th century. The probability of hatching success was markedly variable, and often very low before this synchronization occurred, but became stably high thereafter. Our findings suggest that the stabilizing effect of this synchrony on fitness was indispensable to the recent population increase of *C. facialis*.

Key words: climate change, *Cryptotympana facialis*, hatching success, match/mismatch, phenology, population increase

INTRODUCTION

There are clear global fingerprints of climate change on various ecosystems (Hughes, 2000; Stenseth et al., 2002; Walther et al., 2002). A phenological shift of life cycle events in organisms is one of the most remarkable biological responses to climate warming (Peñuelas and Filella, 2001; Parmesan and Yohe, 2003; Root et al., 2003). When a shift disrupts synchrony between life cycle requirements and availability of seasonally limited resources, it leads to serious consequences for populations. Much effort has been devoted to elucidating the processes and effects of such asynchronization, but has been restricted to its impact on trophic interactions (Harrington et al., 1999; Stenseth and Mysterud, 2002; Visser and Both, 2005). Some authors reported that predator requirements deviated from the peak of prey availability due to heterogeneity in their phenological responses to climate change (Dewar and Watt, 1992; Inouye et al., 2000; Visser and Holleman, 2001). Others showed coincidence of a phenological shift with a population

decline (Both et al., 2006; Ludwig et al., 2006). However, the extent of temporal mismatches (generally described as the number of days between mean/median dates of the “coinciding” phenomena (Russel and Louda, 2004)) is not a simple variable influencing fitness. Changes in relative food abundance can override the effect of temporal mismatches (Durant et al., 2005, 2007). Moreover, other coincidental changes, including food quality and migration patterns, also modulate effects of the temporal interaction (Cannon, 1998; van Asch and Visser, 2007; Post et al., 2008). The complexity of such trophic interactions prevents researchers from linking a temporal mismatch directly to fitness consequence(s), and from describing the actual process through which recent climate change has impacted a population through a phenological shift.

In the present report, we document a causal process by which phenological advancement due to climate warming has directly affected fitness of the cicada *Cryptotympana facialis* (Walker) through a simple non-trophic relationship, i.e., that between hatching time and the rainy season. In Osaka, Japan, there was a drastic change in the species composition of cicadas in the latter half of the 20th century: *C. facialis*, which was initially distributed predominantly in southern regions of Japan, has increased, whereas the other native cicadas have declined (Cyranoski, 2007;

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Supplemental material for this article is available online.
doi:10.2108/zsj.28.875

Numata and Shiyake, 2007). The population of *C. facialis* was formerly a small part of the cicada community, but now constitutes more than 80% of the population at the majority of census sites examined in Osaka (Shiyake, 2004; Takakura and Yamazaki, 2007). During this period, air temperature in Osaka increased by 0.29°C per decade, probably due to the global warming trend and the urban heat island phenomenon. The relationship of decreasing winter severity to the population increase of *C. facialis* was ruled out in our previous study (Moriyama and Numata, 2009), and no causal relationship of warming to the compositional change has been proposed.

Eggs of *C. facialis* are laid in dead twigs overwinter in diapause, and hatch in the next summer (Kato, 1956). We showed previously that after completion of embryonic development, hatching is triggered by high humidity derived from rain (Moriyama and Numata, 2006). However, prolonged arrest of hatching impairs hatchability (Moriyama and Numata, 2010). Thus, for successful hatching, completion of embryonic development must be timed to coincide with a season with frequent rain. The hatching time of *C. facialis* depends on thermal accumulation after overwintering and occurs around the latter half of the early-summer rainy season, i.e., mid-July, in Osaka now (Moriyama and Numata, 2008). This suggests the possibility that recent warming has advanced the hatching time of *C. facialis* to coincide with the rainy season, resulting in improved hatching success.

To clarify how such warming has impacted *C. facialis* fitness, we examined the possible impact on the fitness of *C. facialis* of synchrony between its hatching time and the rainy season by shifting the completion time of embryonic development, and by supplying water at various intervals. We next addressed whether the documented warming in the 20th century could plausibly have caused a phenological shift that could explain the change in synchrony, and how fitness has been affected. Based on the thermal unit for postdiapause development previously described (Moriyama and Numata, 2008), we developed a predictive model, and estimated past hatching times using meteorological records compiled over the last eleven decades (1901–2009). The results showed that climate warming improved the synchrony in the late 20th century, stabilizing the hatching success of *C. facialis*.

MATERIALS AND METHODS

Hatching dates of five cicadas

Eggs of five native cicada species in Osaka Prefecture were obtained from adult females captured between July and early September in 2004–2008: *C. facialis* was from the campus of Osaka City University (34.6°N, 135.5°E, about 10 m a.s.l.), *Graptopsaltria nigrofuscata* (Motschulsky) was from Utsubo Park (34.7°N, 135.5°E, about 10 m a.s.l.), Osaka City, *Meimuna opalifera* (Walker), *Platypleura kaempferi* (Fabricus), and *Hyalessa maculaticollis* (Motschulsky) were from Mt. Hiraoka (34.7°N, 135.7°E, about 300 m a.s.l.), Higashi-Osaka City, Japan. Captured females were individually caged in clear plastic pots with two sticks of *Albizia* wood as oviposition substrates (Moriyama and Numata, 2008). Twigs with overwintered *C. facialis* eggs were also collected on the campus of Osaka City University (Moriyama and Numata, 2006). The sticks harboring eggs were kept under conditions of exposure to the weather of Osaka, and the number of hatching individuals

was recorded as described in a previous study (Moriyama and Numata, 2006).

Control of hatching time and wetting frequency

Twigs bearing oviposition marks of *C. facialis* were collected on the campus of Osaka City University in early February, 2007, when daily mean temperatures were still lower than the lower thermal threshold for postdiapause embryogenesis of *C. facialis*, i.e., 14.31°C (Moriyama and Numata, 2008). Twigs were cut into pieces less than 15 cm in length, and divided randomly into nine groups on 17 February. These twigs were kept at 10°C under 12 h light and 12 h dark cycles (LD 12:12) to prevent embryonic development. The nine groups of twigs were transferred to 25°C and LD 16:8 at intervals of half a month from 5 March to 6 July, and after incubation for 57 or 58 days, they were placed outdoors. Consequently, the nine groups of twigs with developed embryos were exposed to natural weather at intervals of half a month from 1 May to 1 September. In the group transferred outdoors on 1 August, some twigs were kept on an outdoor shelf protected from rainfalls, and submerged into tap water for 1 min at various intervals. After we counted all of the hatched nymphs, the twigs were dissected to assess the remaining eggs that had not hatched. We excluded 2–9 nymphs in some groups that hatched during the 25°C incubation period from analyses.

Estimation of hatching time in the past

The time of the completion of embryonic development was estimated based on temperature records and concepts of thermal requirements (Trudgill et al., 2005). We previously examined *C. facialis* embryogenesis under laboratory conditions, and determined the thermal constants for postdiapause embryonic development and showed their applicability for predicting hatching time in the field (Moriyama and Numata, 2008). To take individual variations of hatching time into consideration, we used that previous experimental data set and selected a cumulative distribution model according

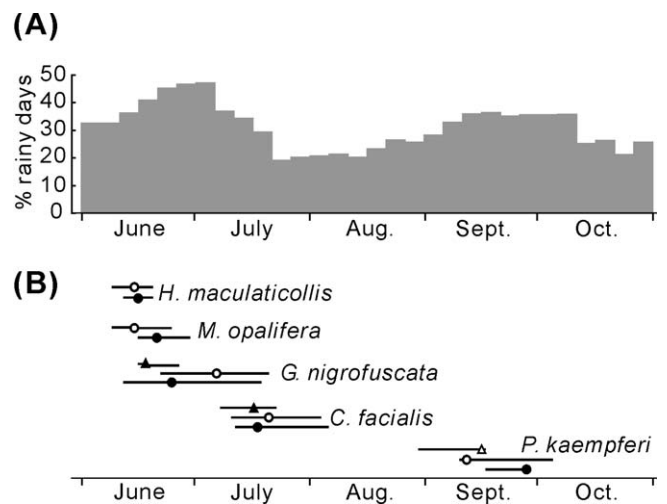


Fig. 1. Differences in hatching time among five cicada species, *Hyalessa maculaticollis*, *Meimuna opalifera*, *Graptopsaltria nigrofuscata*, *Cryptotympana facialis* and *Platypleura kaempferi*. (A) Seasonal fluctuation in the incidence of rainy days, 1901–2009. Data are shown for every five days. (B) Distribution of the hatching time of these five cicadas in Osaka from 2005 to 2008. Eggs of the upper four species hatched after overwintering, whereas those of *P. kaempferi* hatched in the year of oviposition. Open triangles, closed triangles, open circles, and closed circles designate the median hatching dates in the 2005, 2006, 2007, and 2008, respectively, with bars covering 5–95% of hatching. $n = 245$ –1470 for each.

to Akaike's information criterion (Table S1). Hatching probability (P) at a given sum of effective temperatures (SET) above the base temperature (14.31°C) was best-fitted to a skewed sigmoid function (Régnière, 1984):

$$P_{(SET)} = \{1 + \exp[-K(SET - C)]\}^{-1/Q}$$

Three parameters, K , C , and Q , were estimated by a least-square method using R (var. 2.11.1, R Development Core Team 2010). Records of daily temperature measured by the Osaka District Meteorological Observatory from 1901 to 1960 were compiled from several publications (Table S2), and those from 1961 to 2009 were derived from a database on the homepage of the Japan Meteorological Agency (2011). The observatory moved twice (in 1933 and 1968), and the discontinuity of temperature records due to these moves was compensated for according to the method proposed by the Japan Meteorological Agency. SET calculated from daily mean temperatures was assigned to the above logistic function to estimate hatching probability on any given date. To assess the reliability of the predictive model, estimated hatching dates were compared to actual hatching dates observed in the 2006–2008 period (Table S3). Even after completion of embryogenesis, the hatching date is somewhat influenced by daily weather conditions in actual situations. Nevertheless, the estimated hatching dates reliably tracked the actual hatching dates in the field, except 95% hatching dates, probably because opportunity for hatching became scarce after the end of the rainy season (mid-July).

Records of daily precipitation (1901–2009) and the period of the rainy season (1951–2009) were also collected from the database on the website referred to above.

RESULTS

Difference in hatching time among five cicadas

To clarify the significance of the synchrony between hatching and the rainy season, we first surveyed the hatching time of five native cicada species in Osaka. Figure 1 shows the temporal distribution of hatching, as well as the frequency of rainy days. Whereas the eggs of *P. kaempferi* hatched in autumn without overwintering, eggs of the other four species hatched early the next summer after overwintering. As reported in *C. facialis* (Moriyama and Numata, 2006), nymphs hatched in response to rain in all investigated species. *H. maculaticollis* and *M. opalifera* had the earliest hatching time (June). The hatching time of *C. facialis* was the latest among the species with overwintering eggs, and occurred around the end of the early-summer rainy season. In *P. kaempferi*, eggs laid in July hatched mainly in September, when the autumn rainy season generally occurred. No species had a hatching peak in August, when the frequency of rain was the lowest between June and October. This implies the possible importance of taking advantage of the rainy season to hatch in these cicadas.

Fitness consequence of synchrony between hatching and the rainy season in *C. facialis*

To confirm the effects of synchrony between hatching time and rainy season on the hatching success of *C. facialis*, the hatching time window,

when embryogenesis has already been completed and nymphs can hatch in response to rain, was artificially shifted by controlling the rate of development. Nine groups of twigs harboring eggs at a nearly complete stage of embryogenesis were transferred to the outdoors at intervals of half a month from 1 May to 1 September in 2007. The weather in 2007 showed a typical pattern: The rainy season occurred between June and mid-July, followed by the period with scarce rain (Fig. 2A). Artificial shifting of the hatching time window had significant effects on hatching success (Fig. 2B). The hatching times of the first to fourth groups coincided mostly with the period of frequent rain, resulting in high hatching rates of approximately 70%. However, the groups transferred to the outdoors on 1 and 16 July seldom received rainfall after mid-July, and their total hatching rates were approximately 45%. In the group transferred on 1 August, the eggs suffered dry conditions for a long period. Although there was a slight rainfall of less than 0.5 mm on 4 August, it was insufficient to stimulate hatching, and eggs

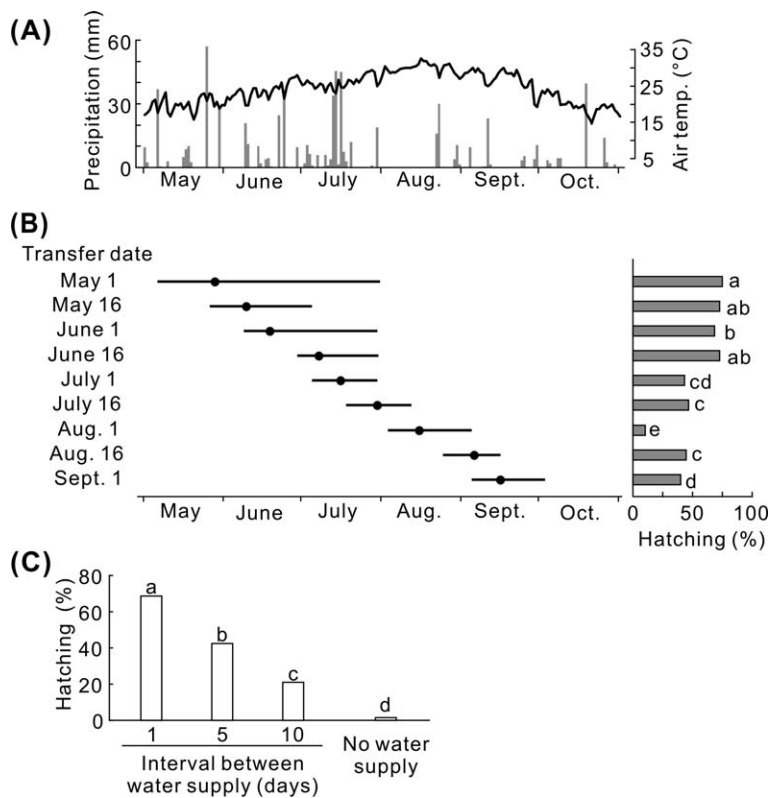


Fig. 2. Effects of synchrony between the hatching time and the rainy season on hatching success in *Cryptotympana facialis*. (A) Daily air temperature (solid line) and precipitation (bars) in Osaka during the experimental period in 2007. (B) Distribution of hatching times and hatching rates as a consequence of the artificial shift in phenology. After controlling embryonic development in the laboratory, twigs containing eggs whose embryogenesis was nearly completed were transferred outdoors at intervals of half a month. Closed circles designate the median hatching dates, with bars covering 5–95% of hatching. $n = 1227\text{--}3490$ for each treatment. (C) Effects of wetting frequency on the hatching rate. Twigs with eggs whose embryogenesis was nearly completed were transferred to an outdoor shelf protected from rainfall on 1 August, 2007, and wetted at various intervals. $n = 1054\text{--}2296$ for each treatment. Hatching rates with the same letters on the right side (B) of histograms and the top (C) are not significantly different ($P > 0.05$, Tukey-type multiple comparisons for proportions, Zar, 2010).

did not receive a substantial rain until 22 August. Only 1.8% eggs responded to the two successive rainy days, suggesting that most eggs had already lost the ability to hatch. In this group, the total hatching rate was only 10%. The hatching rates in the later groups that received rain in late August and September were 40–45%. Despite the high frequency of rain, the hatching rates of these groups were lower than those of early groups, probably because of excessive extension of the embryonic period by the experimental procedure.

Next, twigs that had been transferred to the outdoors on 1 August were wetted artificially at various intervals under protection from natural rainfalls (Fig. 2C). The hatching rate depended strongly on the frequency of supplying water. In the group with daily wetting, it reached approximately 70%, but the longer intervals resulted in the lower hatching success. These results showed a negative effect of temporal mismatch between the hatching time and the rainy season, and a critical role of rain frequency in cicada fitness.

The current warming synchronized hatching time of *C. facialis* to the rainy season

To examine the influence of warming on the synchrony of hatching time with the rainy season, we adopted a predictive model (Régnière, 1984) for completion time of *C. facialis* embryogenesis based on the thermal physiology of postdiapause embryogenesis (Moriyama and Numata, 2008), and we estimated the distribution of the past hatching time between 1901 and 2009 using air temperature records in Osaka (Fig. 3). The estimation showed an obvious phenological shift, accompanied by large inter-year variations (Fig. 3). A regression analysis of median hatching date showed a significant trend of advancement ($r^2 = 0.551$, $F_{1,107} = 131.5$, $P < 0.001$), to the extent of 16.7 days during the 109 years. Whereas a major fraction of eggs were likely to hatch in August in the early 20th century, the estimated hatching peaks shifted to early July in some years of the 1990s and 2000s.

The Japan Meteorological Agency determined the periods of the early-summer rainy season after 1951 (<http://www.jma.go.jp/jma/index.html>), except the onset date in 1963 and the end date in 1993, which were not determined due to the obscure transitions. The onset date was 7 June on average, ranging from 22 May to 25 June, and there were no significant shifts ($r^2 = 0.022$, $F_{1,56} = 1.286$, $P = 0.262$). Figure 3 shows the later extent of the rainy season together with the estimated hatching time. The end date showed a statistically significant backward trend ($r^2 = 0.072$, $F_{1,56} = 4.369$, $P = 0.041$) in 1951–2009, although it varied largely from year to year. Due largely to the warming-driven advancement in hatching time and to a lesser extent due to the prolonged rainy season, the overlap of hatching time with the rainy season increased in the late 20th century. Decadal averages of the proportion of eggs synchronized with the rainy season from the 1950s to 2000s were 6.6%, 14.7%, 23.7%, 47.7%, 51.8% (except 1993), and 82.5%, respectively.

Synchrony with the rainy season stabilized hatching success

We have demonstrated that the advancement

in hatching dates could improve synchrony with the rainy season over the long term. However, considerable annual variations in temperature and precipitation are expected to influence the degree of synchrony and effects of the mismatch on fitness of cicadas. What remains to be clarified is the actual process of the fitness change due to the phenological shift in Osaka. We aligned the hatching probability function to precipitation records at resolution of 1 day over 109 years. As a direct measure governing the hatching success, we computed the number of days from the completion of embryogenesis to the first encounter with precipitation of 1 mm or more. Figure 4 shows the proportions of eggs that had a chance to hatch within 10 days. Before the 1990s, these proportions varied considerably from year to year, and were significantly lower than those after 1990s (Welch's test, $t = 2.74$, $P < 0.01$). The two most critical years were 1912 and 1923. The hatching time window opened within the no-rain period lasting 27 days and 36 days in 1912 and 1923, respectively. In contrast, the years in which more than 50% of eggs received rain within 10 days have continued over 24

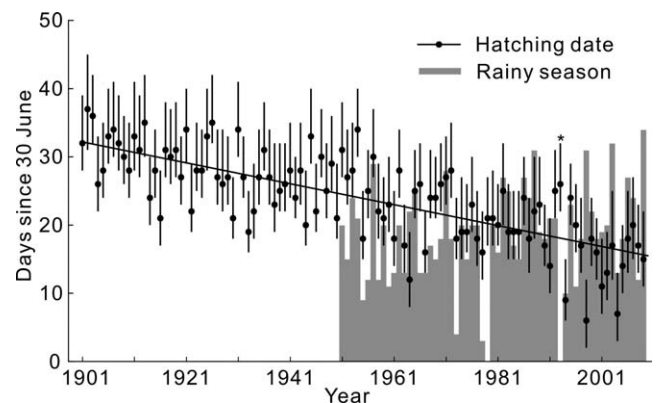


Fig. 3. Phenological relationship between the estimated hatching period of *Cryptotympana facialis* and the early-summer rainy season in Osaka during 1901–2009. Past hatching distribution was estimated by a predictive model, $P_{(SET)} = \{1 + \exp[-0.029 (SET - 592.8)]\}^{-1/0.040}$, and meteorological records. Closed circles designate the median hatching dates, with bars covering 5–95% of hatching. There was a significant trend of median hatching date (line, $r^2 = 0.551$, $F_{1,107} = 131.5$, $P < 0.001$). The latter extent of the rainy season is shown after 1951 (grey columns). * The end date of the rainy season was not determined in 1993.

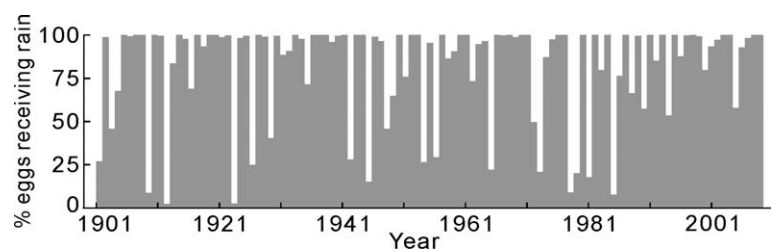


Fig. 4. Change in the estimated hatching success of *Cryptotympana facialis*, 1901–2009. Proportions of eggs expected to receive rain within 10 days from completion of embryonic development were computed from estimated hatching dates (see Fig. 3) and precipitation records in Osaka.

successive years from 1986, which is considerably longer than any other period in the 20th century. Thus, we conclude that warming stabilized hatching success, rather than improving it gradually.

DISCUSSION

For a wide variety of organisms, conditions suitable for certain activities prevail only during a limited period of the year (Harrington et al., 1999; Stenseth and Mysterud, 2002). Activities associated with large fitness consequence are particularly expected to be timed during the period of optimal conditions. Most studies on phenological synchrony have claimed the importance of the timing of juvenile life (Stenseth et al., 2002; Visser and Both, 2005). In the present study, we addressed the hatching time of cicadas in relation to the rainy season. Just after hatching on aboveground parts of plants, cicada nymphs burrow into the soil to establish themselves on suitable rootlets (Beamer, 1928; Myers, 1929). This transition into the soil is a very difficult task for nymphs due to dangers of predation and desiccation on the ground, and is thus one of the most critical periods in the cicada life cycle (Itô and Nagamine, 1982; Karban, 1984, 1997). The trait of hatching triggered by rain ensures that nymphs can avoid the dangers on the ground by burrowing rapidly into the wet, soft soil (Moriyama and Numata, 2006). Laboratory experiments, however, have shown that prolonged arrest of fully developed embryos by continuous low humidity reduces the hatchability, probably due to depletion of energy or water reserves (Moriyama and Numata, 2010). The present study demonstrated a clear consequence of synchrony between hatching time and the season with frequent rain in the field. Mistiming of hatching relative to the rainy season reduced the hatching rate from approximately 70% to 10% (Fig. 2B), and this reduction was fully abrogated by artificial wetting (Fig. 2C). These results support the notion that rain frequency is a primary cause when phenological shifts affect the fitness of *C. facialis* and other cicada species in which egg hatching is triggered by rain.

The early-summer rainy season, which is referred to as "Baiu" in Japan, is derived from a stationary front that extends from the southeastern foot of the Tibetan Plateau to the Japan Islands (Ninomiya and Akimoto, 1992). In central Japan, this period typically prevails between the beginning of June and mid-July, and is characterized by moderate, frequent rain (Ninomiya and Akimoto, 1992; Japan Meteorological Agency, 2002). However, once it ends, subtropical anticyclones bring hot and low-rainfall weather until the autumn rainy season begins (Japan Meteorological Agency, 2002). Our estimation of the *C. facialis* hatching time revealed that it is plausible that the extent of actual warming in Osaka resulted in advancement of the hatching time from the low-rainfall season into the early-summer rainy season in the late 20th century (Fig. 3). Although this synchrony ensured hatching success (Fig. 4), the hatching time lay in the marginal phase of the early-summer rainy season even in the 21st century. According to the 109-year records of precipitation, if nymphs had completed their embryogenesis in late June, the possibility that they would not have received rain within 10 days was less than 1%. This possibility, however, increased to 9.0, 17.8, and 17.2% in early and late July, and early August, respectively. Thus, the

hatching time of *C. facialis* in Osaka in recent years has been heading toward synchronization with the rainy season. It is predicted that warming will continue in the 21st century (IPCC, 2007), and that it will expand the early-summer rainy season by changing water vapor flux (Kusunoki et al., 2006). This would in turn establish firm synchrony of hatching time and the rainy season.

The cicada community in Osaka experienced a drastic change in the late 20th century, and the population of *C. facialis* increased exclusively (Numata and Shiyake, 2007). In this period, Osaka experienced urban development, and many physical and biotic environments change coincidentally with marked warming. Several studies have tried to link these environmental changes to the recent increase in the proportion of *C. facialis* in the cicada community. Mitigation of winter severity by warming did not improve the overwintering success of this species (Moriyama and Numata, 2009). Humidity decline in Osaka is advantageous for hatching success of *C. facialis*, but its influence on the population increase of this species seems to be negligible (Moriyama and Numata, 2010). Predation pressure for *C. facialis* in urban areas did not differ from that in suburban areas assuming the circumstance before the community alternation (Takakura and Yamazaki, 2007). Although adults of *C. facialis* show some preference for host trees, they can exploit a broad range of plant species as a food source and an oviposition material (Kato, 1952). Therefore, the change in flora is unlikely to cause the massive increase of *C. facialis*. On the other hand, some environmental changes associated with urbanization, such as habitat fragmentation (Takakura and Yamazaki, 2007) and soil compaction (M. Moriyama and H. Numata, unpublished data), are likely to affect negatively the other members in cicada community of Osaka. However, its indirect effect on *C. facialis* through biotic interactions remains unclear. In the present study, we demonstrated that phenological mismatch between hatching time and the rainy season led fitness unstable and often caused failed years. Such unfavorable conditions may endanger population persistence (Parmesan et al., 2000; McLaughlin et al., 2002), and seem to have hampered population increase of *C. facialis* before warming. The latest hatching time among the four species in which eggs hatch after overwintering implies that *C. facialis* is a warm-adapted species, because a warmer climate is required to achieve synchrony with the rainy season. In fact, *C. facialis* has a more southern distribution than the other three species, and dwells exclusively in lowland (Kato, 1956; Hayashi, 1984). Therefore, we conclude that although the warming in Osaka favored *C. facialis* in the cicada community in various aspects, the phenological synchrony was an indispensable history to the recent population increase of this species.

The concept that climate change substantially impacts populations of organisms by disrupting the synchrony of organisms' requirements with resources is widely accepted (Stenseth and Mysterud, 2002; Visser et al., 2004). However, it is unlikely that fitness changes steadily along the trend of climate change, because many climatic factors have considerable annual variations compared to the long-term trend. For example, regarding the mean temperature of the growing season of *C. facialis*, i.e., May to August, in Osaka, differences between two consecutive years were $0.58 \pm$

0.40°C (mean \pm SD) in the 1901–2009 period, whereas the warming trend was only 0.021°C per year (Japan Meteorological Agency, 2011). Moreover, conditions of resources may also fluctuate annually, affecting fitness of their exploiters as well as synchrony. The clear causal relationship of rain to hatching success in *C. facialis* enabled us to describe how actual warming has altered cicada fitness for the past 109 years according to the meteorological records. Our results demonstrate that a change in the degree of synchrony by climate change influenced fitness stability against annual variation in temperature and resource conditions. The consequences of temporal mismatch become more serious in years of bad resource conditions. This would seem to apply not only to simple non-trophic systems, but rather appears likely also to contribute to fitness change in more complex trophic systems. In trophic interactions, annual variations in conditions of food resources, such as quality and abundance, also have substantial influence on fitness (Bezemer and Jones, 1998; Cannon, 1998; Durant et al., 2005). Synergy of these annual variations can cause tremendous changes of fitness even if climate change leads to relatively small phenological shifts in the long-term mean. Our findings here regarding fitness change may aid in elucidating the detailed mechanisms by which climate change-driven phenological change influences populations and community structures.

ACKNOWLEDGMENTS

We thank Elizabeth Nakajima for linguistic corrections.

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(Received May 19, 2011 / Accepted June 14, 2011)