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Delayed phenological timing of dragonfly emergence in Japan over five decades

Hideyuki Doi*

LAFWEDY, Faculty of Agriculture, Ehime University, 3-5-7, Tarumi, Matsuyama, 790-8566 Ehime, Japan
*h-doi@agr.ehime-u.ac.jp

Recent increases in air temperature have affected species phenology, resulting in the earlier onset of spring life-cycle events. Trends in the first appearance of adult dragonflies across Japan were analysed using a dataset consisting of observations from 1953 to 2005. Dynamic factor analysis was used to evaluate underlying common trends in a set of 48 time series. The appearance of the first adult dragonfly has significantly shifted to later in the spring in the past five decades. Generalized linear mixing models suggested that this is probably the result of increased air temperatures. Increased summer and autumn temperatures may provide longer bivoltine periods and a faster growth rate; thus, the second generation, which previously hatched in summer, can emerge in the autumn causing the size of the population of dragonflies that emerge in spring to decrease. It is also possible that reduced dragonfly populations along with human development are responsible for a delay in the first observed dragonflies in the spring. However, human population density did not appear to strongly affect the appearance date. This study provides the first evidence of a delay in insect phenological events over recent decades.

Keywords: climate change; global warming; life cycle; Odonata; oviposition; temperature

1. INTRODUCTION

Recent global warming has affected the phenological events of a variety of species, especially in early spring (Parmesan & Yohe 2003; Root *et al.* 2003). A meta-analysis of 143 recent studies reported that most phenological events are occurring earlier in the spring as a result of temperature increases caused by global warming in the past decade (Root *et al.* 2003). Conversely, Gordo *et al.* (2005) showed delayed phenology in the migration of birds over recent decades.

The emergence of insects is an important phenological event because the timing of insect mating is critical for population maintenance (Corbet 1980). In addition, numerous predator–prey interactions are based on the timing of insect emergence (e.g. Nakano & Murakami 2001). Aquatic insects such as dragonflies exhibit early emergence when air temperature increases (Harper & Peckarsky 2006; Hassall *et al.* 2007); however, the

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voltinism flexibility model of dragonflies does not predict early emergence as a result of increasing air temperatures (Braune *et al.* 2008). Furthermore, emergence shifts induced by climate change may cause the mismatch of the intra- and interspecific interactions, which could decrease the population density of the species (Winder & Schindler 2004; Gordo & Sanz 2005; Doi *et al.* in press). The goal of this study was to examine long-term changes in the emergence events of a dragonfly species in Japan and to discuss the role of climate change in these events.

2. MATERIAL AND METHODS

(a) First appearances of dragonflies

I used the datasets of first appearances of adults of the dominant dragonfly *Orthetrum albistylum speciosum* (common skimmer) collected by the Japan Meteorological Agency (JMA, 1985). The life cycle of *O. a. speciosum* is bivoltine, with the larval stage occurring throughout the winter followed by the continuous emergence from April or May to November (Japanese Society of Environmental Entomology & Zoology 2005). The oviposition period is also continuous from late spring to autumn, with the first generation emerging in the early spring. The larvae inhabit ponds, lakes, paddy fields and small streams in both rural and urban areas (Ishida *et al.* 1988). Ban & Kiritani (1980) reported that larvae were mainly observed during July and August in a paddy field. Koch & Suhling (2005) suggested that the eggs of *Orthetrum* do not undergo a hibernation period over the winter.

The JMA has recorded the first appearance of adult *O. a. speciosum* in and/or around each JMA observation station. I selected 48 of 101 stations which have recorded for more than 35 years (31.6–39.4° N, 128.5–140.5° E, see appendix in the electronic supplementary material) for the analysis. Some stations such as those in the Hokkaido region, the Ryukyu Islands, and others within cities with high human populations such as Tokyo and Osaka had fewer than 35 years of data available. The first emergence data were recorded from 1953 to 2005.

(b) Climate and human population data

Air temperature data provided by the JMA from 1953 to 2005 were used to evaluate the effect of climate on the timing of dragonfly appearance. Given that spring and autumn represent the late instar to emergence stage and oviposition to early instar stage of *O. a. speciosum*, respectively (Ishida *et al.* 1988), temperatures were calculated using four mean values for each of the 48 sites during spring (March–May), summer (June–August), autumn (September–November) and winter (December–January).

The human population at each JMA observation site was used to estimate the human impact on phenological changes. Dobson *et al.* (1997) showed that human population density is a good indicator of the human impact on wild populations. The human populations of the city at each JMA site in 2005 were provided by the National Statistics Center of Japan (<http://www.e-stat.go.jp/>).

(c) Statistical analyses

Dynamic factor analysis (DFA) was performed to analyse temporal changes in the first appearance of *O. a. speciosum*. Generalized linear mixed models (GLMMs) were used to estimate the effect of temperature on the first appearance. Details of the DFA and GLMM are provided in the electronic supplementary material. The models were selected using the Akaike information criterion. Single regression analyses were performed to test for correlations between variables and phenological timing, and to analyse the trend of temperature increasing.

3. RESULTS

The spring and summer mean temperatures showed a significant increase between 1953 and 2005 ($r^2=0.236$ and 0.177 , respectively, $p<0.01$, figure 1a), and temperatures in autumn and winter increased significantly throughout the study period ($r^2=0.222$ and 0.140 , respectively, $p<0.01$, figure 1b).

The date of the first appearance of *O. a. speciosum* tended to be delayed from early to mid-May (figure 1c,d). The difference in emergence date from the first observation year to the final year (i.e. 1953–2005 at

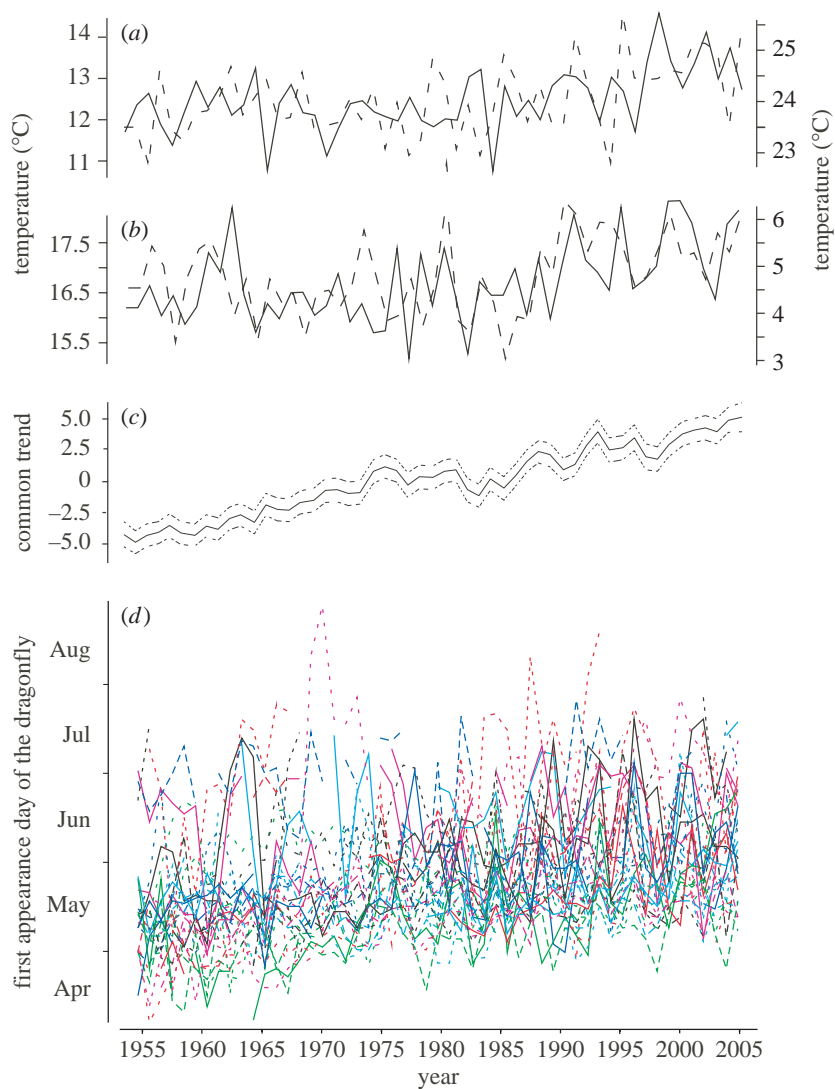


Figure 1. (a) Mean spring (solid line) and summer (dotted line) temperatures at 48 observation sites from 1953 to 2005. (b) Mean autumn (solid line) and winter (dotted line) temperatures at 48 observation sites from 1953 to 2005. (c) The common trends from the common trend 1 model of DFA. (d) Temporal changes in the first appearance day of *O. a. speciosum* from 1953 to 2005. Each line indicates an observation site.

31 sites) was 24.4 ± 28 days (mean ± 1 s.d.) during this time period. Common trend 1 was the best model to explain this trend by DFA (table S1 in the electronic supplementary material). Common trend 1 was significantly positive ($r^2 = 0.920$, $p < 0.0001$, $n = 53$, figure 1c), and factor loadings for common trend 1 were positive at 43 of 48 sites across Japan (figure 2), indicating that dragonfly appearance was delayed at these sites. The factor loadings showed no correlation with latitude and human population density (see figure S1 in the electronic supplementary material). The regression slope between the appearance date and year varied (figure 2), and the regression slope and latitude were significantly correlated, whereas the regression slope and human population density were not (figure 1 in the electronic supplementary material).

The effects of temperature on the responses of phenological timing were estimated using GLMMs (table 1). Temperatures in summer and autumn had a strongly positive correlation with the first appearance, and in winter the correlation was slightly positive. Conversely, temperatures in spring were negatively correlated with the first appearance.

4. DISCUSSION

The analysis showed that the first recorded appearances of adult *O. a. speciosum* occurred significantly later in the year from 1953 to 2005, indicating that the emergence timing of the dragonfly has been delayed. These results differ from those reported by Hassall *et al.* (2007), which suggested an advancement of dragonfly emergence timing in the UK. This may be due to differences in the voltinism of the dragonfly species examined. Specifically, *O. a. speciosum* is bivoltine, whereas the species studied by Hassall *et al.* (2007) were uni- or semi-voltine. I also found that the delay in emergence was enhanced at higher latitudes. This is in accordance with a hypothesis proposed by Braune *et al.* (2008) who predicted that with increasing temperatures the phenology of dragonflies inhabiting higher latitudes will change more than that of dragonflies at lower latitudes.

One possible reason for the delay in dragonfly emergence as a result of temperature increases is a shift in the dragonfly life cycle. Braune *et al.* (2008) predicted that the voltinism of a dragonfly would change with increasing air temperatures. The life

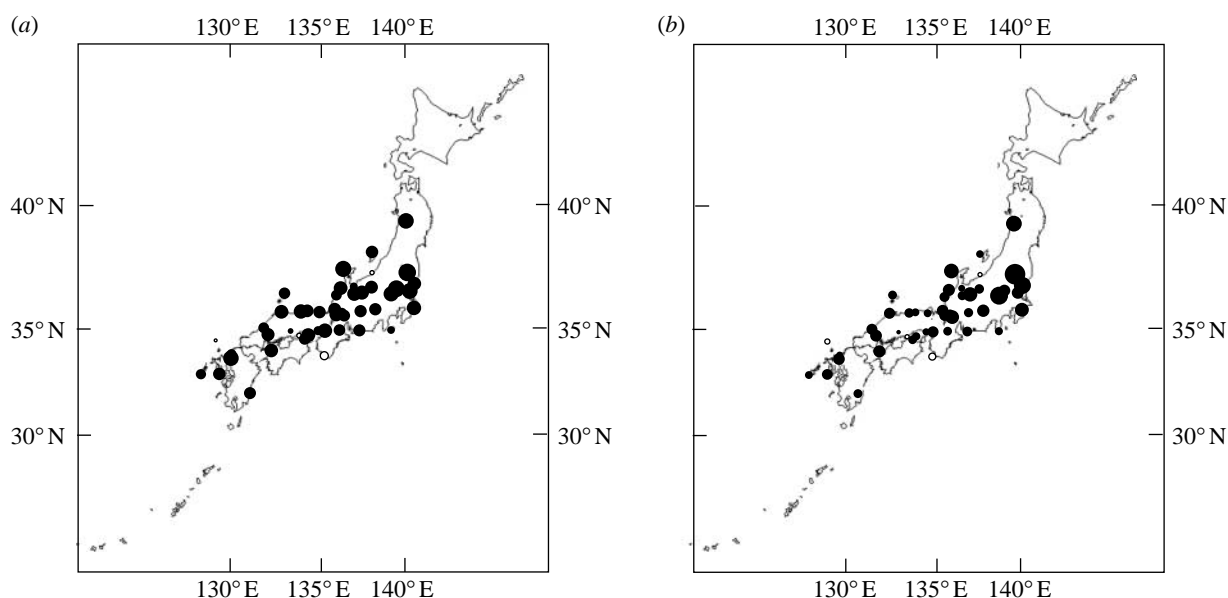


Figure 2. (a) Factor loading (Z) of common trends. The size of the circles indicates the value of factor loading. Open circle indicates negative factor loading. (b) Regression slope (day yr^{-1}) between the first appearance date of the dragonfly and year. The size of the circles indicates the value of the slope. Open circles indicate a negative slope.

Table 1. Coefficients of the temperature in each season of the GLMM. s.e.: mean standard error.

factors	coefficient	s.e.	t -value
spring	-1.62	0.48	-3.37
summer	1.31	0.44	3.00
autumn	2.42	0.48	5.08
winter	0.14	0.40	0.36
(intercept)	92.21	8.81	10.47

cycle of *O. a. speciosum* is basically bivoltine, with emergence occurring continuously from April or May to November. The first generation usually emerges from summer to autumn and the second generation, which hatches in late summer and autumn, emerges in the following spring. However, increasing summer and autumn temperatures may provide longer bivoltine periods and a faster growth rate; thus, the second generation, which previously hatched in summer, can emerge in the autumn causing the size of the population of dragonflies that emerge in spring to decrease. This would result in delayed emergence of the larvae in spring, even though larval development may be faster under higher temperatures in spring.

Another possible explanation for the apparent phenological delay is a reduction of dragonfly population sizes. Tryjanowski & Sparks (2001) showed that the advancement of the recorded arrival date of a bird species was related to increases in breeding population sizes, which allow for a higher probability of observing an early individual in a larger population. These results showed that human population density did not significantly affect the date of dragonfly appearance. The results of this study raise many questions about the long-term changes in dragonfly populations across Japan. However, this is a correlative study, and therefore experiments are needed to

test the effects of temperature and anthropogenic influences on the emergence timing of dragonflies.

The life cycles of most species have been reported to exhibit shifts forward (i.e. cycles are faster or occurring earlier in the year) as a result of temperature increases caused by global warming (Root *et al.* 2003). However, I found that the emergence timing of a common dragonfly has shifted in the opposite direction over the past several decades. That is, although temperatures have significantly increased, the date of the first recorded dragonfly appearance in early spring has been delayed by approximately 24 days. This may have substantial implications for dragonfly populations as well as whole ecosystems, as such changes could lead to changes in the timing of important ecological events such as mating, thereby altering the natural balance of the ecosystem.

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