



# Synergistic effect of daily temperature fluctuations and matching light-dark cycle enhances population growth and synchronizes oviposition behavior in a soil arthropod



Maartje Liefting\*, Jarno Cosijn, Jacintha Ellers

Animal Ecology, Faculty of Earth and Life Sciences, De Boelelaan 1085, 1081 HV Amsterdam, VU University Amsterdam, The Netherlands

## ARTICLE INFO

### Article history:

Received 4 August 2016

Received in revised form 8 October 2016

Accepted 10 October 2016

Available online 14 October 2016

### Keywords:

Circadian rhythm

Natural entrainment

*Orchesella cincta*

Egg laying

Reaction norm

## ABSTRACT

Some major aspects of insect life, like development time and reproduction, can benefit from fluctuating temperatures rather than a constant temperature regime. The benefit of fluctuating temperature has generally been attributed to the non-linear properties of the relationship of many life history traits with temperature. Daily temperature rise, however, usually coincide with the light phase of the photoperiodic cycle and there could be a benefit in linking daily temperature fluctuations with light and dark phases e.g. to anticipate the change in temperature. Such synergistic effects have primarily been studied in the light of activity patterns and gene expression, but have not yet been shown to extend to population dynamics and aspects of individual fitness like oviposition behavior. We therefore explored possible synergistic effects on life history traits of the springtail *Orchesella cincta*. We first test the primary effect of ecologically relevant temperature fluctuations of different amplitudes on population growth and total population mass. The slowest population growth was observed in the constant temperature regime treatment and the highest population growth in the regime with high amplitude fluctuations. In a second experiment, population growth and oviposition rhythm were measured under four different regimes; a constant light and temperature regime, thermoperiod only, photoperiod only and thermoperiod and photoperiod aligned as under natural conditions. The regime in which thermoperiod was aligned with photoperiod resulted in a higher population growth than could be realized by either factor alone. Also, significantly fewer eggs were laid in the constant temperature/light regime than in the other three regimes, strongly suggesting that this regime is stressful to *O. cincta*. Additionally, the fraction of eggs laid at night was highest in the regime with the combined temperature and light cycle. In conclusion, our results show that under these experimental conditions there is a synergistic effect of daily temperature fluctuations in combination with light/dark phases that can considerably influence important life history traits and affect behavior. Such effects are likely to be relevant under natural conditions.

© 2016 Elsevier Ltd. All rights reserved.

## 1. Introduction

Population viability and individual fitness crucially depend on the extent to which organisms can cope with environmental variation in conditions such as temperature, precipitation and nutrient availability. For ectotherms, variation in temperature is particularly important since temperature affects nearly every aspect of their life history (Blanckenhorn, 2000; Fischer et al., 2003; Stillwell and Fox, 2005). Many traits are sensitive to temperature, which is reflected in the shape of the thermal reaction norm of a trait. But even if the reaction norm is known, performance under

fluctuating thermal conditions cannot easily be deduced from it. Several studies have pointed out that exposure to a fluctuating thermal regime can significantly alter the expression of a trait compared to a constant regime with the corresponding mean temperature (reviewed in Beck, 1983; Brakefield and Mazzotta, 1995). When fluctuating temperatures do not exceed performance thresholds, positive effects of fluctuating regimes are commonly found (Beck, 1983; Behrens et al., 1983; Ragland and Kingsolver, 2008). For instance, insects are able to develop at lower average temperatures when temperature is fluctuating diurnally than at constant temperature (reviewed in Stoks et al., 2005). Also, development time is generally shorter when insects are reared under daily fluctuating temperatures than under constant conditions with a comparable mean temperature (Brakefield and Kesbeke, 1997; Davis et al., 2006; Fischer et al., 2011).

\* Corresponding author.

E-mail address: [m.liefting@vu.nl](mailto:m.liefting@vu.nl) (M. Liefting).

The benefits of a daily fluctuating temperature regime have been attributed to specific properties of non-linearity in the relationship between many life history traits and temperature (the reaction norm), referred to as Jensen's inequality or the Kaufmann effect (Kaufmann, 1932; Ruel and Ayres, 1999). Typically, thermal reaction norm shape is concave up in the lower part of the curve, and concave down near the optimum temperature. As a consequence, a temperature increase in the lower part of the reaction norm leads to a larger increase in trait values than a similar temperature decrease causes trait values to go down. When temperature variation spans the lower part of the reaction norm the average trait value will therefore be higher than in a constant thermal regime with the same average temperature, explaining the positive effects of fluctuating regimes as described above. Vice versa, over the higher part of the temperature curve this effect should be reversed, which has indeed been found in a number of species (Bryant et al., 1999; Ragland and Kingsolver, 2008), although exceptions are also commonly found (e.g. Zhao et al., 2014). Overall, Jensen's inequality has been important in understanding the response to temperature variation in ectotherms (Martin and Huey, 2008; Ruel and Ayres, 1999) but other factors are likely to play an additional role.

The relevance of other factors facilitating enhanced performance under fluctuating temperatures have received less attention, but may be equally important, such as adjustments in gene expression, changes in behavior and metabolism, optimization of enzyme functioning and membrane fluidity (see review by Beck, 1983; Clarke, 2003; Dodd et al., 2005; Pernet et al., 2007; van Dooremalen et al., 2011; Williams and Somero, 1996). A key factor that should be considered in this context is the presence of a light-dark cycle. Because temperature rise almost always coincide with the light phase of the photoperiodic cycle under natural circumstances, entrainment of the circadian rhythm to the light-dark cycle automatically projects the fluctuations in temperature, allowing organisms to anticipate the change in conditions behaviorally and physiologically. For example, cyanobacteria and higher plants gain a competitive advantage when the endogenous period is matched to the light-dark cycle (Dodd et al., 2005; Woelfle et al., 2004). Photoperiod can also trigger temperature stress resistance, with shorter day lengths inducing more cold-tolerant and longer day lengths more heat-tolerant phenotypes in a fly species (Fischer et al., 2012). It remains to be tested whether there is an added effect of temperature fluctuations and the presence of a light-dark cycle. Previous studies on the interaction effect of photo- and thermoperiod primarily focused on patterns in gene expression rhythms and locomotor activity rhythms in individual organisms (Constantinou and Cloudsley-Thompson, 1985; Currie et al., 2009; Fuchikawa and Shimizu, 2007; Moore and Rankin, 1993; Yoshii et al., 2009), but did not extend the effects to life history traits and population dynamics.

Here, we explore the effects of a daily temperature gradient and presence of a light-dark cycle and to what extent these parameters act synergistically, in the springtail *Orchesella cincta*. Springtails are a globally significant group of organisms that play a major role in soil functioning (Rusek, 1998), particularly through their effect on the rate of litter decomposition and nutrient fluxes (Cragg and Bardgett, 2001). We first test the effect of amplitude of temperature fluctuations on population growth and total population mass of *O. cincta*. We additionally consider population growth and oviposition rhythm under four different regimes that differ in light and temperature cycles; thermoperiod only and constant light, photoperiod only and constant temperature, thermoperiod and photoperiod aligned as under natural conditions, and a constant light and temperature regime. This allows us to test if fluctuating temperature and light-dark cycle each have an independent effect or if they act synergistically when aligned as under natural

conditions. If the effect of thermoperiod is the only explaining factor, Jensen's inequality is sufficient to explain an enhanced effect of temperature fluctuations, whereas if the effect of thermoperiod is influenced by the presence of a light cycle, this may be informative on possible synergistic effects of both a light and dark phase and temperature fluctuations.

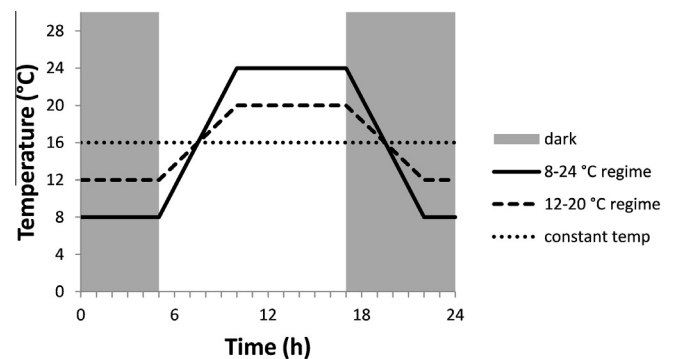
## 2. Materials and methods

### 2.1. Study organism

*Orchesella cincta* (Collembola) is a wingless arthropod that lives in soils rich in organic matter and is found in the litter layer in a broad range of habitats in the Holarctic (van Straalen et al., 1985). Like all Collembola, *O. cincta* grows indeterminately, with moults separating instars. Springtails used in the temperature amplitude experiment were collected at the Kampina Nature Reserve in the Netherlands and kept in the lab in a climate chamber at a mildly fluctuating regime (12/20 °C with 7 h at the maximal and minimal temperature, 70% RH, LD 12:12 h, temperature would rise with the start of the light phase and descend with the start of the dark phase) for approx. 3 generations. Springtails used in the thermo- and photoperiod regime experiment were collected from the Roggebotzand forest in the Netherlands and kept in a climate room at a constant regime (15 °C, 70% RH, LD 12:12 h) for approx. 6 generations before the start of the experiment.

### 2.2. Effect of amplitude of temperature fluctuation on population growth and mass

Three thermal regimes were set up in three different climate rooms; two with fluctuating temperatures and one with constant temperature (Fig. 1). Temperature fluctuations were sinusoidal to mimic moderate and more extreme natural conditions in natural habitats of *O. cincta* (Liefing and Ellers, 2008). The minimum and maximum temperatures were chosen based on data collected in the litter layer of forest and heath habitats in the summer of 2006 (data not shown). The more extreme range of 8–24 °C is based on temperatures in the heath litter layer during summer, where temperatures may drop to 7 °C at night and reach 27 °C during the day over a short time span. The minimum and maximum temperatures of 8–24 °C are not within the optimal thermal range of *O. cincta* when measured under constant conditions and although these temperatures are likely experienced regularly by springtails in the field, a continuous exposure to such a high amplitude of temperatures deviates from natural conditions. However,



**Fig. 1.** Temperature and light-dark regimes as used in the population growth experiment under fluctuating temperatures of different amplitudes. The three temperature regimes represent a fluctuating temperature cycle with high amplitude (8–24 °C), low amplitude (12–20 °C) and constant temperature (16 °C). A light-dark cycle of LD 12:12 h was implemented during all three temperature regimes with the start of the light interval coinciding with the start of the temperature rise.

Download English Version:

<https://daneshyari.com/en/article/5593243>

Download Persian Version:

<https://daneshyari.com/article/5593243>

[Daneshyari.com](https://daneshyari.com)