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Contrasting the potential effects of daytime versus nighttime warming on insects

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Mean increases in temperatures associated with climate change are largely driven by increases in minimum (nighttime) temperatures; however, most climate change studies disproportionately increase maximum (daytime) temperatures. We review current literature to compare the potential effects of increasing daytime and nighttime temperatures on insects and their interactions within ecological communities. Although few studies have explicitly addressed the effects of nighttime warming, we draw from broader literature on how insects are affected by temperature to identify possible mechanisms that the timing (day or night) of warming may affect insects. Specifically, we discuss daily temperature variation, thermal performance curves, behaviour and activity patterns, nighttime recovery from hot days, and bottom-up effects mediated by plants. Although limited, the existing evidence suggests nighttime and daytime warming can have different effects, and thus we encourage scientists to use the most realistic warming treatments possible to truly understand how insects and their communities will be affected by climate change.

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Introduction

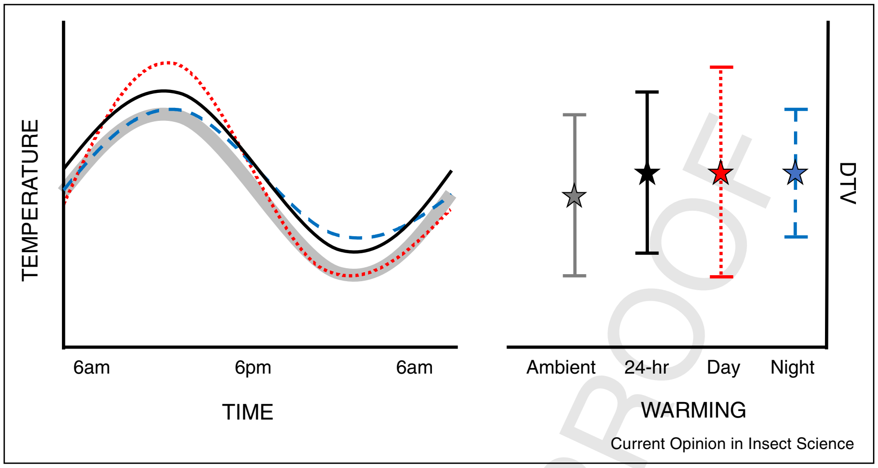
Mean global surface temperatures have been increasing since the last century and are expected to increase an additional 2–4 °C by the end of the 21st century [1]. However, the way in which mean daily temperatures increase can be driven by several different patterns of warming [2]. First, temperatures could increase by the same amount uniformly throughout a 24-hour cycle. Thus mean temperature may increase but there would be no effect on daily temperature variation (DTV; the variation in temperature that organisms experience through the day; Figure 1). Alternatively, warming may occur asymmetrically throughout a 24-hour cycle. For example, the majority of warming could occur during the daytime, with nighttime temperatures increasing little or not at all. In this case, mean temperature would increase, as would DTV. This approach is common in warming studies because (1) many experiments use solar energy to manipulate temperature treatments (e.g., greenhouse effect or shading to create cooled conditions), or (2) researchers are specifically interested in the effects of increasing frequency of extreme heat events. Although there is much evidence to demonstrate that increases in the frequency of extreme heat events and the associated increase in DTV have important ecological consequences (see Stoks *et al.*, in review, this issue), elevated daytime temperatures are not driving the general trend of increasing mean global temperatures. Instead, historical datasets and models suggest that mean temperatures are increasing through a third mechanism, where nighttime temperatures are increasing at a faster rate than daytime temperatures [1,3•,4]. Although daytime and nighttime warming could produce the same increase in mean daily temperature, nighttime warming will decrease DTV and may differ from daytime warming in other ecologically important ways.

Although increasing nighttime temperatures may be driving much of global warming, this detail is largely ignored in ecological studies, often 'for the sake of simplicity' [5]. To illustrate this point, we reexamined papers from a recent review on climate change and trophic interaction experiments [6], and found that none of the 158 studies on temperature effects considered nighttime warming (but see Vangansbeke *et al.* [7], which manipulated DTV in a way that is informative about the effects of nighttime warming). Most warming studies examined the effects of uniform warming or daytime-biased warming. In other words, to study the effects of a 2.5 °C increase in mean temperature, most studies would either increase temperatures 2.5 °C above ambient throughout the entire day, or increase daytime temperatures (e.g., 06:00 to 18:00 h) by 5 °C with no change during the night. Although these studies are informative about the effects of elevated temperatures and extreme heating events, they may be less informative about the effects of chronic increases in mean temperature that are driven by warming nights associated with climate change.

Reasons why the effects of daytime and nighttime warming may differ

To explore why and when the timing of warming may matter, we briefly review some of the ideas and evidence

Figure 1



Relative to an ambient diurnal temperature cycle (thick grey line), mean daily temperature (indicated with a ★ on the DTV plot) can be increased in several ways. Temperatures can be warmed above ambient by a constant amount (solid black line), which does not change daily temperature variation (DTV) relative to ambient. Many climate change studies disproportionately increase daytime temperatures (e.g., 6am to 6pm; dotted red line), which increases daily temperature variation (DTV) experienced by an insect. By contrast, much of climate warming experienced during the 20th century and that forecasted for the future has been driven by disproportionately increasing nighttime temperatures (e.g., 6pm to 6am; dashed blue line), which decreases DTV.

already established about how insects respond to temperature. Specifically, we address daily temperature variation (DTV); non-linear temperature performance curves (TPCs); the role of nighttime as a heat stress recovery period; how behaviour and activity patterns vary throughout the day; and the indirect bottom-up effects mediated by plants.

Daily temperature variation (range)

In recent years, the entomological literature has focused on the effects of increasing daily temperature variation (DTV), sometimes referred to as daily temperature range (DTR) [7–11,12••]. Many of these studies change temperature by increasing T_{high} and decreasing T_{low} by the same amount, which alters DTV but keeps mean temperature constant among DTV treatments [7–10,12••]. Although in general they do not explicitly express interest in nighttime warming, these experimental designs can provide some insight into how daytime and nighttime warming may have different effects on insects and their communities.

The effects of increasing DTV are highly context dependent, but a large amount of literature demonstrates that increasing DTV has ecologically-relevant consequences for insects (see Stoks *et al.*, this issue for a thorough review of the current literature). Increasing DTV can directly affect insects, altering performance traits such as metabolic rate, body size, life span, fecundity and more [13•]. Additionally, increasing DTV can affect a wide variety of interactions, including competition [14], predation [7,8], herbivory, and symbiosis (Stoks *et al.*, this issue). Since increasing DTV has been shown to affect insects and their interactions in many ways, it stands to reason that nighttime warming, which decreases DTV, is also likely to affect those interactions, but in different ways. However, this hypothesis remains untested.

Temperature (thermal) performance curves

The effects of temperature on trait performance can be conceptualized using thermal performance curves (TPCs) [15]. The relationship between a given trait (e.g., feeding rate, body mass, survivorship, among others) and temperature usually takes the shape of an asymmetrical curve, gently rising from a minimum critical temperature (CT_{min}) to a thermal optimum (T_{opt}) then decreasing rapidly towards the maximum critical temperature (CT_{max}) [16] (Figure 2). TPCs reveal several reasons that insects may be affected differently by daytime and nighttime warming. First, due to the nonlinear nature of TPCs, the magnitude of a warming effect may differ at different temperatures because the slope of the curve is not constant. Thus, changing temperatures near CT_{min} may have less of an effect on performance than increasing temperatures near T_{opt}, where the slope of the line is generally steeper. Second, the direction of the effect (positive or negative) may differ at different temperatures. Increasing low temperatures (T_{low}) may increase trait performance by moving away from CT_{min} and towards its T_{opt}, while the same magnitude of warming for high temperatures (T_{high}) could quickly push an individual over T_{opt} and towards (or beyond) their CT_{max} (Figure 2), where they are unable to survive or reproduce [17].

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