IN FOCUS
Predicting responses to climate change requires all life-history stages

The bog fritillary butterfly (*Bolaria eunomia*) alights onto *Persicaria bistorta*. This species of butterfly can be found in bogs, moist tundra, and willow seeps throughout the north-temperate region of the Northern Hemisphere. Photo: Camille Turlure.

In Focus: Radchuk, V., Turlure, C. & Schtickzelle, N. (2013) Each life stage matters: the importance of assessing response to climate change over the complete life cycle in butterflies. *Journal of Animal Ecology*, **82**, 275–285.

Population-level responses to climate change depend on many factors, including unexpected interactions among life history attributes; however, few studies examine climate change impacts over complete life cycles of focal species. Radchuk, Turlure & Schtickzelle (2013) used experimental and modelling approaches to predict population dynamics for the bog fritillary butterfly under warming scenarios. Although they found that warming improved fertility and survival of all stages with one exception, populations were predicted to decline because overwintering larvae, whose survival declined with warming, were disproportionately important contributors to population growth. This underscores the importance of considering all life history stages in analyses of climate change's effects on population dynamics.

With increasing availability of long-term abiotic and biotic datasets, it is becoming clear that human-induced climate change has had, and will continue to have, real and irreversible impacts on Earth's physical and biological systems (Pachauri & Reisinger 2007; Solomon *et al.* 2009). Climate change has increased air and water temperatures, pushed local precipitation regimes towards their extremes, and amplified frequencies of extreme weather events (Pachauri & Reisinger 2007). These physical changes, in turn, have had biological impacts over multiple scales. For example, changes in phenology (e.g. earlier breeding, spawning, flowering and migration) and demographic rates (e.g. increased mortality) have been observed. At broader scales, researchers have noted altered species interactions as the result of, for example, mismatches in previously synchronized phenologies among species or shifting geographical distributions, new invasions as habitat characteristics evolve, and new instances of diseases in warmer or wetter climates. These changes, among others, are predicted to cause population declines and extirpations, distributional range shifts, species extinctions and altered community structures (Walther *et al.* 2002; reviewed in Bellard *et al.* 2012). Climate change-related impacts have been observed across all taxonomic groups (reviewed in Walther *et al.* 2002) and are considered major threats to species world-wide.

*Correspondence author. Email: szeigler23@gmail.com

For effective species recovery planning, it is critical to understand the nature of threats and the mechanisms behind them – information that is often lacking (Lawler *et al.* 2002). Quantitative demographic models have been advocated as powerful tools for understanding avenue(s) through which a given threat acts on a species or population (Schemske *et al.* 1994). For example, sensitivity or elasticity analyses of such models can be used to identify the life-history stage or demographic process with the greatest impact on population growth rate, which can then be used to design conservation strategies (e.g., Crouse, Crowder & Caswell 1987; Schemske *et al.* 1994). In this issue, Radchuk, Turlure & Schtickzelle (2013) use a combination of laboratory and/or field experiments and deterministic periodic matrix models to predict how climate change, specifically through increases in temperature, could impact populations of the vulnerable bog fritillary butterfly (*Boloria eunomia*).

In laboratory and/or field experiments, the authors examined the number of eggs laid by females as well as the survival of various stages at increasing temperature regimes (15–27 °C). They found that increasing temperature enhanced fertility and survival of eggs, pre-diapause larvae, and pupae but decreased survival of overwintering larvae. They then used experimental fertility and survival rates to parameterize deterministic periodic matrix models under four scenarios reflecting variation in how climate change could alter temperature (i.e. constant increase in temperature, increase in winter and spring temperatures only, and high and low extremes in temperatures throughout the year). Sensitivity analyses of the baseline matrix model demonstrated that the species was most vulnerable to changes in survival of overwintering larvae. Because increasing temperature adversely affected this life-history stage in laboratory experiments, the population was predicted to decline quickly under all climate change scenarios. The population declined the most (by 97%) under the scenario where temperature increased only during winter and spring months, which is the climate change pattern predicted for the European region where *B. eunomia* is found (Christensen *et al.* 2007).

This study is significant for a number of reasons. It empirically demonstrates the effect of warmer temperatures and global climate change on a threatened species. Understanding how a species will respond to extreme events related to climate change, such as marked temperature increases, is a major challenge in the natural sciences but is necessary for predicting the future behaviour up to the ecosystem-level (Jentsch, Kreyling & Beierkuhnlein 2007). Thus, sound experimental approaches that contribute to this understanding, as exemplified by Radchuk, Turlure & Schtickzelle (2013), are critical. In addition, most climate change-related research has focused on 'trend effects' (i.e. changes in mean climatic values); however, 'event effects' (i.e. changes in frequency of extreme climatic events) may have a greater and more immediate effect on species and ecosystems (Jentsch, Kreyling &

Beierkuhnlein 2007). While few studies have focused on the impacts of these event effects, Radchuk, Turlure & Schtickzelle (2013) do so by using their periodic matrices to explore scenarios that include high and low extremes in temperature throughout the year.

Finally, and most importantly, this study is particularly valuable in that it demonstrates the need for examining the impact of an extrinsic threat like climate change over all life-history stages. Although other studies have shown that it is important to analyse climate change's impact over the full life cycle of a species because the impacts of climate change can interact with other extrinsic drivers and intrinsic vital rates to produce counterintuitive outcomes (Adahl, Lundberg & Jonzen 2006), few researchers actually do so (reviewed in Radchuk, Turlure & Schtickzelle 2013). Radchuk, Turlure & Schtickzelle (2013) validate this concept elegantly with their use of experimental and modelling approaches. Even though experimental results showed that increased temperatures would have a positive impact on fertility and survival of all life history stages with one exception, populations of *B. eunomia* were instead predicted to decline because the stage most sensitive to increased temperature had a disproportionately large impact on population dynamics. Thus, had only one or a few vital rates been examined, one might erroneously predict that climate change could have a net positive effect on *B. eunomia*. Also, by highlighting which stage in the species' life cycle had the greatest impact on population dynamics, the authors are able to provide recommendations for applied conservation, which they discuss in their article in this issue.

Using a simplified system, Radchuk, Turlure & Schtickzelle (2013) also offer an important foundational perspective on which further, more complex experiments and modelling exercises can be based. For example, determining vital rates for a single experimental 'population' over 1 year for use in periodic matrix models obviously does not capture the spatiotemporal variation in vital rates that can occur between years or across populations in real ecosystems (e.g. Freville *et al.* 2004; Ozgul *et al.* 2006; Angert 2009). Typically, at least 15–20 years of observations are necessary to predict population growth rate or extinction risk adequately (Fagan, Meir & Moore 1999; Holmes *et al.* 2007; Che-Castaldo & Inouye 2011), and similar modelling outputs (e.g. minimum viable population size) are context-dependent results of interactions between a species' life history, environmental conditions and extrinsic threats that can lead to substantial with-in species variation (Flather *et al.* 2011). Thus, Radchuk, Turlure & Schtickzelle (2013) could extend their work by incorporating spatiotemporal variability in the vital rates of *B. eunomia*, potentially illustrating a range of stage- and population-level responses to climate change. In addition, new insights could be made by increasing the complexity of experiments and matrix models. For instance, stochasticity and density feedbacks were not included in the authors' periodic matrix models. Stochas-

ticity is an especially important driver of population dynamics in small populations (Boyce 1992; Ralls, Beissinger & Cochrane 2002; Melbourne & Hastings 2008); environmental stochasticity can decrease long-term population growth rates, demographic stochasticity can create Allee effects and unstable equilibria, and stochastic fluctuations in population size can lead to chance extinctions (Lande 2002). Similarly, density feedbacks can be important drivers of population dynamics and can interact in unintuitive ways with other effects of climate change (Saether, Sutherland & Engen 2004; Adahl, Lundberg & Jonzen 2006). Finally, within the system that *B. eunomia* is a part, climate change could simultaneously impact resource or host plants, native or invasive competitors and predators, leading to altered population dynamics that cannot be predicted by projecting vital rates for the species in isolation. Likewise, other components of global change (e.g. habitat loss and fragmentation, overexploitation, biological invasions) can have synergistic interactions with climate change that lead to substantially greater population declines than would be predicted if each threat was considered alone (Sala *et al.* 2000; de Chazal & Rounsevell 2009). Population models for *B. eunomia* that include interspecies interactions or multiple threats, perhaps using the framework established by Keith *et al.* (2008), could build off of the important initial work by Radchuk, Turlure & Schtickzelle (2013) to provide additional insights into population dynamics for *B. eunomia* under climate change in the future.

SARA ZEIGLER

Department of Biological Sciences, Virginia Tech,
Blacksburg, VA, 24060,USA

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