



# Integrating multiple stressors across life stages and latitudes: Combined and delayed effects of an egg heat wave and larval pesticide exposure in a damselfly



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## ABSTRACT

To understand the effects of pollutants in a changing world we need multistressor studies that combine pollutants with other stressors associated with global change such as heat waves. We tested for the delayed and combined impact of a heat wave during the egg stage and subsequent sublethal exposure to the pesticide esfenvalerate during the larval stage on life history and physiology in the larval and adult stage of the damselfly *Lestes sponsa*. We studied this in a common garden experiment with replicated central- and high latitude populations to explore potential effects of local thermal adaptation and differences in life history shaping the multistressor responses. Exposure of eggs to the heat wave had no effect on larval traits, yet had delayed costs (lower fat and flight muscle mass) in the adult stage thereby crossing two life history transitions. These delayed costs were only present in central-latitude populations potentially indicating their lower heat tolerance. Exposure of larvae to the pesticide reduced larval growth rate and prolonged development time, and across metamorphosis reduced the adult fat content and the flight muscle mass, yet did not affect the adult heat tolerance. The pesticide-induced delayed emergence was only present in the slower growing central-latitude larvae, possibly reflecting stronger selection to keep development fast in the more time-constrained high-latitude populations. We observed no synergistic interactions between the egg heat wave and the larval pesticide exposure. Instead the pesticide-induced reduction in fat content was only present in animals that were not exposed to the egg heat wave. Our results based on laboratory conditions highlight that multistressor studies should integrate across life stages to fully capture cumulative effects of pollutants with other stressors related to global change.

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## 1. Introduction

To understand and predict the effects of pollutants in a changing world we need multistressor studies that combine pollutants with other stressors related to global change such as temperature stress (Hooper et al., 2013; Noyes and Lema, 2015). Such studies are essential to reveal the cumulative impact of global change, as stressors related to global change often interact synergistically (Fischer and Phillips, 2014; Holmstrup et al., 2010; Przeslawski et al., 2015). While multistressor studies with pollutants are steadily increasing in number, several topics remain poorly studied, yet important to fill the need for a more realistic risk assessment of pollutants under warming (Landis et al., 2013; Noyes and Lema, 2015). Extreme

temperatures during heat waves, a major component of recent climate change (Bailey and van de Pol, 2016; Jentsch et al., 2007), can strongly affect organisms (Gardner et al., 2011). Despite recommendations to take into account heat waves when studying global warming (Bailey and van de Pol, 2016; Jentsch et al., 2007; Jentsch and Beierkuhnlein, 2008), few experiments explicitly do so in combination with pollutants (but see e.g., Arambourou and Stoks, 2015; Dinh Van et al., 2016; Janssens et al., 2014).

Stressors may not only have direct but also delayed effects (when the exposure to the stressor ended). As a result, stressors separated in time may still interact in a delayed way with each other (Gunderson et al., 2016; Segner et al., 2014). Most species show a complex life cycle with major transitions between the egg stage, the larval stage where growth occurs, and the adult stage where dispersal and reproduction occur (Moran, 1994). Carry-over effects of stressors may thereby cross life stage boundaries (Metcalf and Monaghan, 2001). Especially, during the egg stage animals may

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have less ability to avoid exposure to stressors such as heat waves (Potter et al., 2011). Yet, studies on carry-over effects of thermal stressors experienced during the egg stage on the sensitivity to pollutants in later life stages are very rare (but see Broomhall, 2004).

Responses to pollutants and thermal stressors can show considerable geographic variation (Clements et al., 2012; Dinh et al., 2016; Dinh Van et al., 2013; Janssens et al., 2014), which may be partly linked to local adaptation and associated changes in life history. Particularly, latitudinal gradients are getting increased attention in the context of thermal stressors given that these make up gradients of temperature (means and extremes) and life history (Stoks et al., 2014). In temperate regions, ectothermic organisms face increasingly limited time to complete the larval stage and reach maturity and reproduce towards the higher latitudes (Gotthard, 2001). These time constraints may cause a faster larval growth and development at higher latitudes (Sniegula et al., 2016a), which may on its turn cause a higher sensitivity to pollutants because of energy allocation trade-offs with defense and repair mechanisms (Congdon et al., 2001). While these mechanisms may cause strong geographic differences in the sensitivity to stressors, multistressor studies with pollutants across latitudes are still rare (but see e.g. Cherkasov et al., 2010; Dinh Van et al., 2013).

Here, we report on a multistressor study where we tested for the delayed and combined impact of a heat wave during the egg stage and subsequent sublethal pesticide exposure during the larval stage on life history and physiology in the larval and adult stages of the damselfly *Lestes sponsa* (Hansemann). We studied this in a common garden experiment with replicated populations from two latitudes to explore effects of local thermal adaptation and differences in life history shaping the multistressor responses. Damselflies are amongst the taxa most sensitive to global warming (Hassall, 2015) and excellent model species to test for ecological and evolutionary principles in ecotoxicology (Stoks et al., 2015). As a pesticide we chose the pyrethroid esfenvalerate, to which damselflies are particularly sensitive (Beketov, 2004). Besides life history traits we also focused on adult traits related to flight ability and dispersal (adult fat content and flight muscle mass) and upper thermal tolerance (CTmax) that are important for fitness in damselflies (Corbet, 1999; Stoks and Córdoba-Aguilar, 2012). While the delayed effects of the egg heat wave for the larval sensitivity to esfenvalerate allow testing 'climate-induced toxicant sensitivity', the delayed effects of larval exposure to esfenvalerate on CTmax allow testing for 'pollutant-induced climate sensitivity' (sensu Noyes and Lema, 2015).

## 2. Methods

### 2.1. Study species

*L. sponsa* is a strictly univoltine (one generation per year) Eurasian damselfly. In central and northern Europe females lay eggs in June–August (Boudot and Kalkman, 2016; Johansson et al., 2010). Eggs enter diapause within a couple of weeks and individuals overwinter in the egg stage. In spring, eggs hatch and larvae develop into adults within 2–3 months. High-latitude populations (northern Sweden) evolved faster larval development and growth rates and highly synchronous egg hatching and adult emergence patterns in response to stronger seasonal time constraints (Sniegula et al., 2016a,b).

### 2.2. Field sampling

We studied two populations each at the high-latitude (northern Sweden, 65°36'21.36"N, 22°7'42.69"E and 65°51'5.26"N, 21°27'49.32"E) and central-latitude (northern Poland,

53°29'38.20"N, 16°30'55.95"E and 53°38'18.18"N, 16°22'27.60"E) regions of the European distribution (Boudot and Kalkman, 2016). These populations were chosen in areas without agriculture, hence they are unlikely to be exposed to pesticides (Coors et al., 2009). In both regions heat waves with air temperatures up to 30 °C have been recorded as early as April (Poland; <http://www.imgw.pl/>) and June (Sweden; <http://www.smhi.se>), with the frequency of air temperatures equal to or exceeding 29 °C being more frequent in Central Europe (Coumou and Rahmstorf, 2012). Therefore, exposure of eggs to the here applied extreme temperature of 29 °C is ecologically relevant in both regions. We expected eggs from central-latitude populations to better deal with thermal stress.

We obtained eggs from adult females between 28 July and 4 August 2015 in the central-latitude populations, and between 9 and 12 August 2015 in the high-latitude populations. These dates correspond to the peak of the flying season at both regions. Females were placed in plastic jars with moist filter paper for egg laying at 22 °C. We obtained egg clutches from 12 and 18 females in the central populations, and from 5 and 8 females in the high-latitude populations. Filter paper with eggs from both regions was sent by regular mail to the laboratory in Leuven. Central-latitude eggs arrived within 7 days and high-latitude eggs within 5 days. Results from previous experiments indicated that this procedure has no effect on life history traits (Sniegula et al., 2012a, 2012b).

### 2.3. Rearing conditions

In the laboratory, egg clutches were submersed in dechlorinated tap water in an incubator at 21 °C and 16:8 L:D to allow pre-diapause development. To simulate winter conditions experienced by eggs in nature, on day 17 after oviposition the temperature was lowered to 15 °C, and on day 19 lowered to 10 °C. On day 21 we adjusted temperature to 4 °C and the light was turned off. On 28 September 2015 the arrival of spring was simulated; for practical reasons we did so simultaneously for all eggs, irrespective of their laying date. On this date the central- and high-latitude eggs were between 55 and 62 and 47–50 days old, respectively. In *L. sponsa*, the duration of simulated winter conditions in the egg stage has no effect on larval life history traits (Sniegula et al., 2016a; Sniegula and Johansson, 2010). At this date, the temperature was elevated to 10 °C and the photoperiod set to 12:12 L:D. On 1 and 10 October 2015 we further increased temperature to 21 °C and 22 °C, respectively, and photoperiod 12:12 and 19.5:4.5 L:D. These temperature changes were rather abrupt. Yet, previous experiments where more gradual temperatures changes were used (Sniegula et al., 2016b; Sniegula and Johansson, 2010), showed similar differences in life history traits between latitudes, indicating that the here applied warming rates did not disrupt normal development.

Immediately after hatching, groups of 10 randomly chosen larvae per latitude were placed together in 180 mL plastic cups filled with 100 mL of dechlorinated tap water to enhance survival (De Block and Stoks, 2003). After two weeks, larvae were placed individually in these same cups until adult emergence. Larvae were fed daily *ad libitum* with *Artemia* nauplii. After entering the pre-final instar, larvae were fed three *Chironomus* larvae three times per week until emergence.

### 2.4. Experimental setup

To test for the single and combined effects of egg exposure to a heat wave and larval exposure to the pesticide esfenvalerate, we set up a full factorial experiment with 2 latitudinal regions (high-latitude/central-latitude) × 2 heat wave treatments in the egg stage (presence/absence) × 2 esfenvalerate treatments in the larval stage (presence/absence). The sample size of each heat wave × esfenvalerate combination varied between 38 and 41 indi-

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