



Latitudinal and age-specific patterns of larval mortality in the damselfly *Lestes sponsa*: Senescence before maturity?



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ABSTRACT

Latitudinal differences in life history traits driven by differences in seasonal time constraints have been widely documented. Yet, latitudinal patterns in (age-specific) mortality rates have been poorly studied. Here, we studied latitudinal differences in pre-adult age-specific mortality patterns in the strictly univoltine damselfly *Lestes sponsa*. We compared individuals from three latitudes reared from the egg stage in the laboratory at temperatures and photoperiods simulating those at the latitude of origin (main experiment) and under common-garden conditions at a fixed temperature and photoperiod (supplementary experiment). Results from the main experiment showed that the high-latitude population exhibited higher mortality rates than the central and southern populations, likely reflecting a cost of their faster development. Age-specific mortality patterns, also indicated higher ageing rates in the high-latitude compared to the low-latitude population, which likely had a genetic basis. The strong within-population variation in hatching dates in the low-latitude population caused variation in mortality rates; individuals that hatched later showed higher mortality rates presumably due to their shorter development times compared to larvae that hatched earlier. In both experiments, larvae from all three latitudes showed accelerated mortality rates with age, which is consistent with a pattern of senescence before adulthood.

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1. Introduction

To understand and predict range shifts under global warming there is an increasing interest in latitudinal patterns in life history (Stoks et al., 2014). Despite this, we have only limited knowledge how a key life history trait, namely ageing differs between latitudes. A major driver of life history evolution that differs between latitudes are time constraints associated with seasonality such as the onset of winter. Under time constraints animals are expected to accelerate development and growth in the larval stage (Abrams et al., 1996). Assuming limited availability of resources, this leads to allocation costs (Arendt, 1997; Cichoń, 1997; Kozłowski and Wiegert, 1987; Mangel and Munch, 2005; Munch and Mangel, 2006), including a reduced investment in maintenance and repair (De Block and Stoks, 2008). This may lead to an accelerated rate of mortality with larval age, hence senescence (Bonduriansky and Brassil, 2002; Dmitriew, 2011). This generates the hypothesis that latitude-associated differences in time constraints will shape latitudinal differences in senescence.

The classic evolutionary theories of ageing suggest that senescence is expected to be observed after maturity, because the force of selection against senescent deterioration is the strongest before the onset of reproduction (Dańko et al., 2012; Dańko and Kozłowski, 2012; Hamilton, 1966). However, selection against early mortality seems to work imperfectly as pre-reproductive mortality is well documented in many species (Gotthard, 2001; Levitis, 2011; Mikolajewski et al., 2005). While these examples have not been linked to senescence, the presence of pre-reproductive senescence is possible as it is a general and inevitable process driven by trade-offs and constraints (Cichoń, 1997; Dańko et al., 2015).

There are two major difficulties to detect the senescence in immature stages. Firstly, extrinsic mortality caused by external factors such as predation and pathogens may favor intrinsic mortality, including senescence (Williams, 1957, but see Abrams, 1993). However, at the same time extrinsic mortality can mask early intrinsic hazard, because the magnitude of the latter one is much lower early in life (Pietrzak et al., 2015). This divergent role of extrinsic mortality motivates the importance of laboratory experiments, because in such experiments environmental conditions can be controlled and the background (extrinsic) mortality minimized (Nussey et al., 2013). Secondly, the intrinsic mortality related to senescence may not be frequently detected by researchers in premature life stages, not only because of the strong

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selection against it, but also because many species have a relatively short juvenile period when compared to adult lifespan. Because senescence is a gradual process, ageing can only be detected over long time periods. One group of animals that gives the opportunity to study a potential presence of senescence before maturation are insects, because many insect species spend most of their life in premature stages (Speight et al., 2008).

In this study we tested for latitudinal differences in pre-reproductive age-dependent mortality rates in the damselfly *Lestes sponsa* (Hansemann) (Odonata, *Lestidae*), a species with longer pre-mature stages than adult stage (Jödicke, 1996). Comparing multiple populations that experience different environmental conditions is a key for better understanding the mechanisms driving age-specific mortality (Carey, 2001; Walsh and Reznick, 2011). Throughout its latitudinal distribution *L. sponsa* is a strictly univoltine (one generation per year), egg-overwintering insect (Corbet, 1999). Larvae react to seasonal time constraints by accelerating development and growth. This is true both for larvae from high-latitude populations that have a much shorter growth season compared to low-latitude populations (Sniegula et al., 2016a; Sniegula and Johansson, 2010), as well as for late-hatched compared to early-hatched larvae at a given latitude (De Block and Stoks, 2005; Stoks et al., 2005). We therefore reared larvae of *L. sponsa* from the egg stage from high-, central and low-latitudes experiencing gradually less time constraints because of increasingly longer growth seasons. In the main experiment, larvae were grown at the temperatures and photoperiods reflecting those at the latitude of origin, while in a supplementary experiment we reared them at a mean constant temperature and photoperiod that corresponded to the average of the three latitudes. The latter allowed to evaluate environmental and genetic contributions in shaping larval mortality patterns (Williams et al., 2006). Part of the data set from this experiment has been used in articles where we

estimated quantitative genetics of life history traits (Sniegula et al., 2016a) and synchrony of phenological events (Sniegula et al., 2016b). Here, we focused on ageing rates. Specifically, we predicted increasing age-specific patterns of mortality rates within each latitude as a result of trade-offs between resource availability for damage repair driven by limited season length. We also expected that more time constrained individuals, i.e. individuals from high latitude populations and individuals that hatched later in the season at a given latitude, will show higher larval mortality in general and higher increases in age-specific mortality rates (hence faster ageing) than less time constrained individuals.

2. Methods

2.1. Study species

L. sponsa is a common European damselfly (Fig. 1). High latitude populations evolved higher larval growth rates than central and southern latitude populations, whereas the difference between central and southern populations is less pronounced, though biologically meaningful (Sniegula et al., 2016a). Females lay eggs during late spring and summer (Jödicke, 1996).

Eggs develop for about two weeks and during this time they reach an advanced embryonic developmental stage. Next, the eggs enter winter in diapause. During the following spring, the timing and synchrony of hatching is regulated by temperature and photoperiod (Corbet, 1956; Sniegula et al., 2016b). Larval development time, measured from egg hatching until adult emergence, takes two to four months (Jödicke, 1996; Sniegula and Johansson, 2010). Development time is shorter at higher temperatures and photoperiods mimicking later dates in the growth season (Pickup and Thompson, 1984; Johansson et al., 2001; Sniegula et al., 2014).

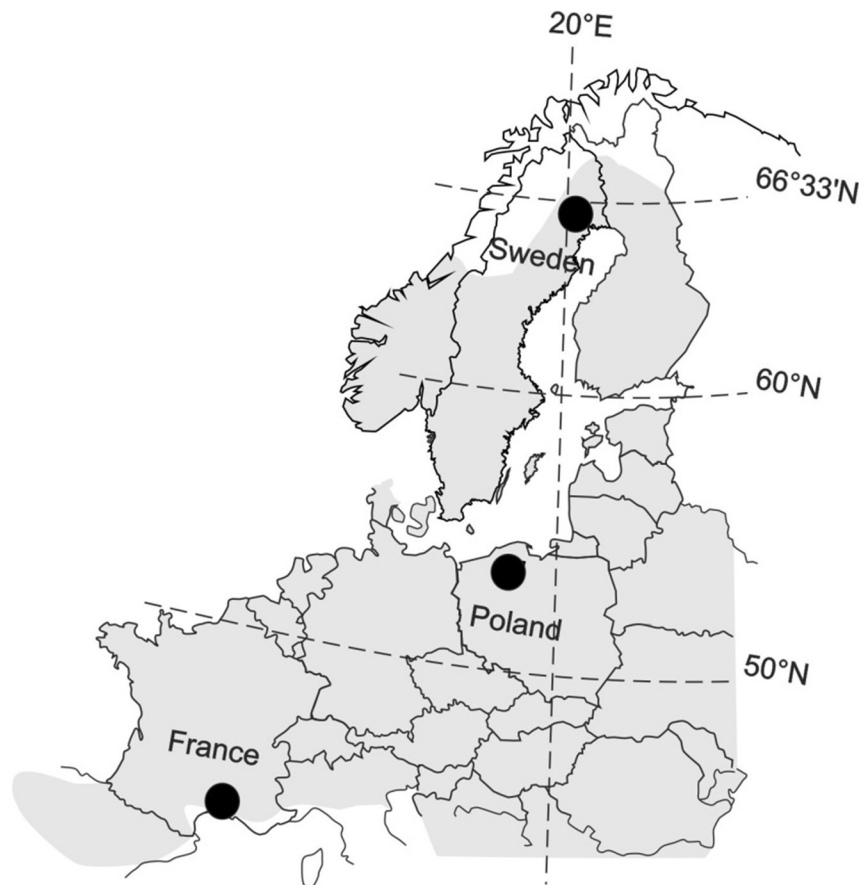


Fig. 1. Map showing the sampled populations (filled circles) and the European distribution of *Lestes sponsa* (shaded area; after Boudot and Kalkman, 2016).

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