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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.

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).

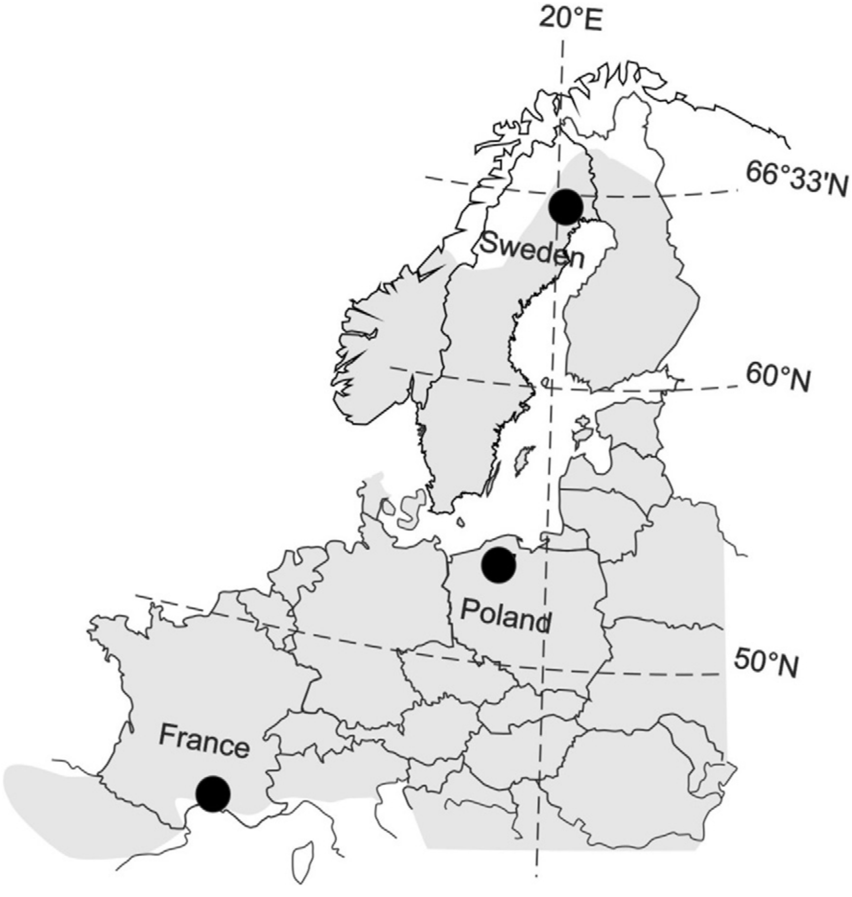

Fig. 1. Map showing the sampled populations (filled circles) and the European distribution of *Lestes sponsa* (shaded area; after Boudot and Kalkman, 2016).

2.2. Field collection and transportation

We collected *L. sponsa* eggs from three latitudes in Europe ranging between 43°30′N and 66°36′N (Fig. 1), and covering a distance of 2730 km. Eggs were received from adult females using a standard method as described in Sniegula et al. (2014). To take into account within-latitude population-specific differences in life-history traits, we sampled two populations in each region. Eggs were sampled from two northern (N), two central (C) and two southern (S) populations (Fig. 1) at following dates: 6–10 August (northern populations), 23–28 July (central populations), and 29 June-2 July 2013 (southern populations). These dates correspond to the peak of the flight season at each latitude (Boudot and Kalkman, 2016). We collected 44 families in the northern populations, 49 families in the central populations, and 54 families in the southern populations. Egg clutches were put inside a Styrofoam box at 22 °C and transported by car to Krakow, Poland. The transportation took one, two and three days from central, southern, and northern populations, respectively. Previous experiments showed that this kind of transportation has no effect on life history traits in *L. sponsa* (Sniegula et al., 2014; Sniegula and Johansson, 2010).

2.3. Laboratory experiment

2.3.1. Main experiment

The aim of the main experiment was to test whether more time constrained larvae (originating from more northern latitudes and late-hatched larvae at a given latitude) have a higher mortality and higher increases in age-specific mortality rates when experiencing temperatures and photoperiods simulating those at their latitude of origin (simulated conditions are shown in Fig. S.I.1). The experiment was performed in the Institute of Nature Conservation PAS, Krakow, Poland. Individuals sampled from northern, central and southern latitudes were separately reared in three climate chambers with programmed temperatures and photoperiods mimicking these variables at each study latitude. To follow natural changes in each study region, we adjusted temperature and photoperiod once a week, except for the winter simulation, described below. Information on water temperatures in shallow parts of ponds, habitat preferred by damselfly larvae (Corbet, 1999), at each region was derived from the extension of the FLake model (Lake Model Flake, 2009; Nilsson-Örtman et al., 2012). For a detailed description of the model see Sniegula et al. (2016a).

Upon arrival at the laboratory, egg clutches were individually placed in plastic containers (12 × 8 cm, 5 cm height) filled with 250 ml of a mixture of dechlorinated tap water and filtered pond water. After 2–3 weeks we started initiating the winter conditions. We lowered temperature to 15 °C and retained the late summer photoperiod. The following day we lowered temperature to 5 °C and turned off the light (24 h of darkness). Such conditions were kept in each chamber for 28 days to simulate natural winter conditions.

We initiated spring arrival by switching to a temperature of 12 °C and the photoperiod associated with the date when water temperature exceeded 12 °C at a given latitude. For the northern sites this corresponded with 30 May, for the central sites with 25 April, and for southern sites with 4 April. Eggs started to hatch approximately 28 days after spring initiation. At hatching, 10 eggs were randomly chosen from each clutch and individually placed in round plastic containers (diameter 7 cm, height 4 cm). This resulted in 434 northern, 467 central, and 527 southern individuals, giving a total of 1428 individuals at the start of the experiment. Larvae were fed daily (between 10:00–12:00 local time) with laboratory reared brine shrimps – commonly used food in laboratory experiments with odonate larvae (Hottenbacher and Koch, 2006; Sniegula et al., 2012). During feeding every larva received on average 350 (SE: 26.8, N = 10) brine shrimp nauplii, which is a high food ratio for *Lestes* larvae (Johansson et al., 2001). We simulated weekly changes in temperature until 25 July (chamber with northern individuals; week 9), 15 August (chamber with central individuals; week 17) and 12 September (chamber with southern individuals; week 24). Under natural conditions, the temperature begins to decrease at these dates. Yet, at these dates there were still individuals that had not emerged (201 northern, 205 central and 13 southern-latitude individuals). We kept the corresponding temperatures constant starting from these dates until the end of the experiment (the chamber with northern individuals at 20.2 °C; with central individuals at 21.0 °C; and with southern individuals at 22.0 °C) to minimize the effect of lower temperature on mortality. The mean temperatures between the termination of winter simulation and the end of the experiment were 19.2 °C for the northern regions, 19.9 °C for the central region, and 21.3 °C for the southern region. The photoperiod followed weekly changes until the end of the experiment. The longest and shortest photoperiods between termination of winter simulation and the end of the experiment were as follows: northern region 24:00–00:00 h and 14:36–09:24 h, central region 18:51–05:09 h and 10:25–13:35 h, and for southern region 16:37–07:23 h and 11:04–12:56 h. More information on temperatures and photoperiods can be found in the Supporting information in Sniegula et al. (2016a).

For all studied latitudes mortality was recorded every third day from hatching to emergence of the last individual. Egg hatching and adult emergence were recorded daily. The experiment was terminated when the last larva emerged or died.

2.3.2. Supplementary experiment

The Supplementary experiment was designed to explore how larvae originating from different latitudes respond in mortality and survival when experiencing a fixed temperature and photoperiod (common-garden conditions; Fig. S.II.1). Results from this supplementary experiment inform about the presence of genetic differences among studied populations for the studied traits. The experiment was carried out in a fourth climate chamber where larvae from all three latitudes were grown together. The supplementary experiment therefore had less replicates than the main experiment. A fixed temperature of 21.9 °C was programmed since all studied latitudes experience this temperature in nature for at least several hours per day during the growth season. A fixed photoperiod of 19:25 light hours was programmed because it corresponded to the longest day length during the growth season at the mid-latitude across the transect of the three sampled latitudes (55°N, 10°E). During the initiation of spring conditions in the main experiment, we randomly chose 5–6 eggs from eight clutches from each latitude and this gave a total of 141 eggs at the start (northern: 47 [19 dead; 28 emerged]; central: 46 [22 dead; 24 emerged]; southern: 48 [9 dead; 39 emerged]). We placed these eggs individually in round plastic containers in the climate chamber. All other experimental procedures were as in the main experiment. Given the low sample sizes, the results of the experiment were treated only as supplementary, and therefore are presented in Supplementary materials (S.II).

2.4. Statistical methods

All analyses were performed in R v3.1.3 (R Development Core Team, 2016). We used the same statistical methods for both experiments, however, some analyses were not performed for the supplementary experiment due to the limited number of replicates (individuals). We assume that all events, i.e. hatching, dying, and emerging, occur in the middle of the particular time interval they were registered.

The survival data were analyzed using the Kaplan-Meier estimator (Moeschberger and Klein, 2005). The individuals that emerged were treated as right-censored. The equality of survival distributions between groups was tested by log-rank tests (Moeschberger and Klein, 2005) in the R-package *survival*. The log-rank test is more sensitive to differences in late occurring events and is most powerful when the hazard ratios are constant (Martinez and Naranjo, 2010). Where multiple comparisons were applied the Holm's correction method for *p*-values (Holm, 1979) using *p.adjust* in the R-package *stat*.

The survival data were fitted with five candidate models typically assumed in survival analysis (Missov et al., 2016; Pletcher et al., 2000; Sherratt et al., 2010) with use of the maximum likelihood approach (Efron and Tibshirani, 1994; Moeschberger and Klein, 2005; Pletcher, 1999). These models include (i) the Exponential model (E) that assumes constant and age-independent hazard and thus is a null model without senescence, (ii) the Gompertz model (G) based on an exponentially increasing hazard with age, (iii) the Gompertz-Makeham model (GM) which is an extension of the Gompertz model that accounts for age-independent background mortality, (iv) the Gamma-Gompertz model (GG) that accounts for unobserved heterogeneity in mortality risk and is defined via logistic hazard, and (v) the Gamma-Gompertz-Makeham model (GGM), which extends the GG model for an age-independent mortality. In the G and GM models age-dependent mortality $\mu(x)$ is an exponential function of age and takes the form: $\mu(x) = e^{a + bx} + c$; where x denotes age, the exponent of the parameter a determines the initial intrinsic age-dependent mortality, b represents the Gompertz exponential coefficient (defined hereafter as the rate of ageing), and parameter c is the Makeham term representing background mortality. When $c = 0$ the GM model reduces to the G model. Although the Gompertz-family of models describes mortality in many populations quite well, it is important to note that it is empirically driven rather than strongly rooted in the biological theory (but see Golubev, 2009; Pietrzak et al., 2015; Strehler and Mildvan, 1960). All above models (except E) assume exponentially (or asymptotically exponentially for $c > 0$) increasing individual mortality rates, however GG and GGM models additionally assume that individuals differ from each other in terms of unobserved frailty (or vitality, Vaupel et al., 1979). Such a heterogeneity leads to bending down the mortality curve in later ages, eventually reaching a plateau (S.III). The GG and GGM models assume the Gompertz function as baseline hazard and gamma-distributed frailty with mean 1 and squared coefficient of variation γ. The resulting hazard of such model is a logistic function defined as: $\mu(x) = [e^{a + bx}] / [1 + \gamma e^{a} (1 - e^{bx}) / b] + c$, where c is the Makeham term (which equals zero in the GG model). The meaning of parameters a and b is the same as in the G and GM models. The additional parameter γ captures the hidden heterogeneity in frailty. For more detailed description of GG and GGM models see Vaupel et al. (1979), Missov et al. (2016) and Vaupel and Yashin (2005). Maximization of the likelihoods was done by differential evolution optimization, using the R-package *DEoptim* (Mullen et al., 2011).

We choose the most parsimonious model based on the AICc model selection criterion (Johnson and Omland, 2004; Pletcher, 1999) and verified this using the hLRT (hierarchical likelihood ratio test) method. The hLRT method used LRT (likelihood ratio test) to compare nested models with increasing complexity. Given that our set of candidate models is only partially nested, the choice between GG and GM models was based on maximized log-likelihood values (both models have the same number of parameters). Simply, the model with a higher log-likelihood value was considered to be superior. For a similar application of the method see Sherratt et al. (2010). The confidence intervals of estimated parameters as well as survivorships and log-mortality curves were calculated analytically using the sandwich estimator (Efron and Tibshirani, 1994). As a goodness of fit measure we used the coefficient of determination proposed by Nagelkerke (1991), with the exponential model (constant hazard, assuming no senescence) as the reference model ("intercept" model).

To pairwise compare parameters of the fitted distributions between latitudes we used likelihood ratio tests (LRT), as proposed by Pletcher (1999), which is more powerful than the comparison of confidence intervals (see above). We used an algorithm which involves the construction of an extended model that includes data of both populations. Under the null hypothesis one of the model parameters is fixed for all populations, while the alternative hypothesis assumes every parameter to be fitted independently. Please note that it is not necessary that compared latitudes were fitted by the same model, because all models are nested and interpretation of parameters is the same.

Given that temperatures and photoperiods differed between latitudes in the main experiment, we considered three time scales to express age when modelling the mortality data. Besides the 'actuarial age' (expressed in days), we also expressed age in degree-days (the sum of the daily experienced temperatures) and in light-days (the sum of experienced light hours divided by 24 h).

We also tested the differences in survival and emergence between early and late hatched individuals by constructing sub-cohorts for the S populations of the main experiment. We considered only S populations because they had sufficient heterogeneity in hatching dates (standard deviation, N: 2.29, C: 8.73, S: 16.49; interquartile range, N: 2.75, C: 12, S: 16). For the S population we divided all larvae into early and late individuals. The threshold hatching dates were chosen arbitrarily to cover both tails of the distribution, and to have similar number of individuals in both groups (see Fig. S.I.2 in Supplementary materials). Choosing other thresholds did not affect the results qualitatively. After assignment, the early S sub-cohort consisted of 97 individuals that hatched before day 27 of the experiment, whereas the late S sub-cohort consisted of 96 individuals that hatched after day 48 of the experiment. Individuals that hatched during middle dates were not included in the analysis. The median temperature and photoperiod experienced with interquartile bounds for both Early and Late sub-cohorts for particular regions are shown in Fig. S.I.3. In each case there is a clear shift in experienced temperatures and degree-days with age.

3. Results

3.1. Survival and mortality

The percentage of larvae that survived till emergence differed between regions: 46.1% of the northern larvae (200 out of 434), 67.9% of the central larvae (317 out of 467) and 53.9% of the southern larvae (284 out of 527).

We found significant differences in survivorship curves between the three latitudes irrespective of the time scale used (actuarial age: $\chi^2 = 96.87$, df $= 2$, $p < 0.0001$; degree-days: $\chi^2 = 141.93$, df $= 2$, $p < 0.0001$; light-days: $\chi^2 = 24.42$, df $= 2$, $p < 0.0001$). For the actuarial age scale the lowest survival was in N, but there was no obvious general trend in survival with latitude as curves crossed (Fig. 2, left panel). The pairwise comparisons identified significant differences between survivorship curves at each latitude (Table 1). Interesting results were obtained in other time scales (summarized in Table 1). In the degree-days scale, the relative pattern of survivorship curves looked qualitatively similar to the actuarial age scale, however the test could not detect differences between the central and low latitude. The transformation of the age scale to light-days resulted in shifting survivorship curves of N larvae towards survivorship curves of C and S larvae, which reduced differences between different latitude populations. This was especially the case when comparing N and S populations, where no significant differences between survival distributions could be detected (but notice that curves crossed rendering the log-rank test less powerful).

Model selection based on AICc and on hLRT indicated that in no case the model without senescence (the E model) was chosen (Table 2, for AICc weights see Table S.I.1). For each latitude a model with increasing mortality rates with age independently of the used time scale was selected. The AICc method selected GG for the northern population (N), GGM for the central population (C), and GM for the southern population (S) and very similar results were obtained by the hLRT selection method (Table 2). The fit of the best fitting models for each latitude under each time scale is shown in Fig. 2. The estimated parameters (MLEs) of the selected models fitted separately to each latitude are shown in Table 3. The comparison of confidence intervals of fitted parameters between different latitudes within a given time scale showed significant

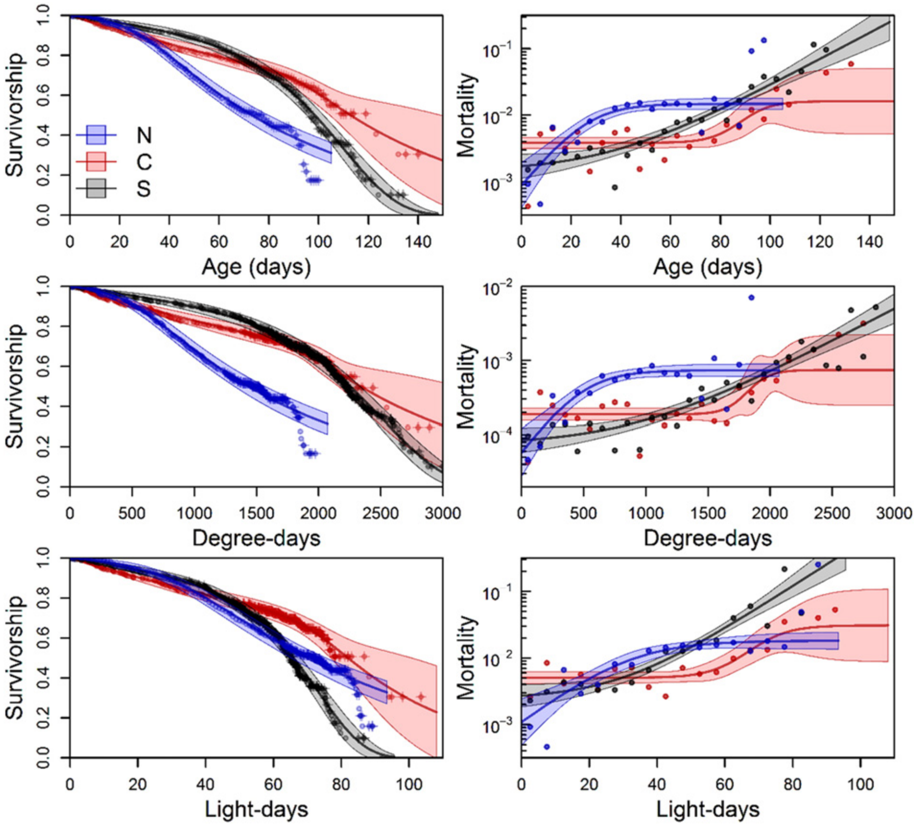

Fig. 2. Age-specific patterns in survivorship (left) and mortality rates (right) of *Lestes sponsa* larvae from three latitudes. Survivorship estimates are based on the Kaplan-Meier estimator of survival (dots); lines connect the estimates from the best fitted model (northern (N): GG, central (C): GGM, and southern population (S): GM). Individuals that emerged were considered censored. Censoring events are indicted by '+' (individual ages at emergence). For visualization, empirical mortality rates are represented by dots that were calculated from 5-day aggregated data for age and light-days, and from 100-degree-day aggregated data for degree-days. Confidence intervals and fitted curves are plotted per latitude until the last observed death.

differences only in background mortality (c). Differences in other parameters could not be detected, because of the very high standard errors of the MLEs of the mortality model for central latitude (C). The less precise estimates for the central latitude may be caused by the high background mortality (c) masking underlying intrinsic mortality patterns (see Pietrzak et al., 2015 for discussion). This is further supported by the very low coefficient of determination for models fitted to C (Table S.I.2). When only comparing the two other latitudes using the likelihood ratio test (LRT) we found significantly higher values for a in the northern (N) than in the southern (S) latitude using degree-days and light-days, as well as significant higher values for the b parameter in N than in S using actuarial age and degree-days (Table 4A, notice the same results via the less powerful method of confidence interval comparison in Table 3A). Additionally, model selection showed parameter γ to be significantly higher than zero in N and C suggesting a strong effect of hidden heterogeneity in individual frailties on marginal mortality rate (Table 2, hLRT).

Table 1
Results of pairwise comparisons of survival distributions between latitudes.

Comparison	Time scale	χ^2	df	p	Holm's p
N vs. S	Age (days)	68.96	1	0.0000	0.0000
N vs. C		64.17	1	0.0000	0.0000
C vs. S		4.76	1	0.0292	0.0292
N vs. S	Degree-days	124.70	1	0.0000	0.0000
N vs. C		75.84	1	0.0000	0.0000
C vs. S		0.03	1	0.8630	0.8630
N vs. S	Light-days	2.89	1	0.0890	0.0890
N vs. C		14.79	1	0.0001	0.0002
C vs. S		26.89	1	0.0000	0.0000

p-Values of log-rank tests were adjusted (Holm's method) for the three comparisons within the same time scale. Abbreviations as in Fig. 2.

3.2. Mortality rate of early and late hatched individuals in the southern population

Survivorship curves of both cohorts in S showed better survival of early-hatched individuals than late-hatched ones both using actuarial age ($\chi^2 = 5.12$, df $= 1$, $p = 0.0236$) and light-days ($\chi^2 = 6.51$, df $= 1$, $p = 0.0107$) (Fig. 3). Although such differences were not found using degree-days for the here applied threshold ($\chi^2 = 1.67$, df $= 1$, $p = 0.1965$), for many other thresholds we also found these differences (close to) being significant (for example, when the threshold was set to <24 days for early-hatched and to >60 days for late-hatched larvae; results not shown). We fitted the most parsimonious mortality model for the total population of S (GM) to both cohorts. The pairwise comparison of GM parameters between early and late cohorts could not detect any significant differences (Tables 3B and 4B).

4. Discussion

At all three latitudes individual mortality rates accelerated with age and were well fitted by models assuming exponential baseline hazard (excluding background mortality and heterogeneity) (see also S.III). These age-specific patterns of mortality were expressed across latitudes despite variation in the temperature and photoperiod conditions that the larvae were grown in and remained when using time scales taking into account the accumulation of degree-days or light-days. Furthermore, in the supplementary experiment (S. II), where both temperature and photoperiod were maintained constant across the experiment, the

Table 2
Maximum log-likelihoods of the five fitted senescence models and the selected model based on AICc and hLRT.

Data	E	G	GM	GG	GGM	AICc	hLRT
N, age	−1341.3	−1306.1	−1306.1	−1296.3	−1296.3	GG	GG
N, degree-days	−2036.2	−2005.9	−2005.9	−1997.7	−1997.7	GG	GG
N, light-days	−1332.1	−1285.0	−1285.0	−1280.0	−1280.0	GG	GG
C, age	−966.1	−963.0	−961.0	−963.0	−959.1	GGM	GGM
C, degree-days	−1421.4	−1419.5	−1417.1	−1419.5	−1414.3	GGM	GGM
C, light-days	−922.2	−917.7	−914.3	−917.7	−913.3	GGM	GM
S, age	−1492.0	−1390.3	−1386.5	−1390.3	−1385.7	GM	GM
S, degree-days	−2251.0	−2157.8	−2152.9	−2157.8	−2152.4	GM	GM
S, light-days	−1395.4	−1291.0	−1285.1	−1291.0	−1284.7	GM	GM

Model codes are given in the methods section. Abbreviations as in Fig. 2.

increasing mortality rates were also present at all latitudes (Fig. S.II.3, top row). Although, such increases in mortality rates with age are considered to indicate senescence in adult stages (Jones et al., 2014; Pietrzak et al., 2015; Ricklefs and Scheuerlein, 2002; Tatar, 1999), here we deal with the pre-reproductive stage, where ageing is not expected. According to the classic evolutionary theories of ageing, senescence is not expected before maturity, because of strong selection against any deterioration that compromises survival. Yet, every cell accumulates damage, because repair mechanisms are not perfect (but see Dańko et al., 2015). This is because the efficiency of tissue repair and maintenance rely on trade-offs between different allocation sinks (e.g. growth) and/or physiological constraints that must take place before maturity, especially if a juvenile period constitutes most part of the total lifespan as in the study species. Furthermore, we documented differences in mortality rates and age-specific mortality rates between latitudes that remained in the supplementary experiment at a common temperature and photoperiod, suggesting a genetic basis for these differences (Fig. S.II.3, Fig. S.II.4).

4.1. Explaining the increasing mortality rates with age

The pattern of increasing (accelerating at the individual level) mortality with age seems to be consistent with the disposable soma theory (Kirkwood, 1977). According to this theory senescence is a result of tradeoffs between somatic maintenance and reproductive gains (here expected only in the future). Because most organisms are constrained by the amount of resources available, selection may favor allocation decisions that indirectly lead to senescence even before an organism reaches maturity. Indeed, such early allocation decisions where shown to be evolutionary optimal in some theoretical models (Cichoń, 1997; Cichoń and Kozłowski, 2000; Mangel and Munch, 2005; Munch and Mangel, 2006). For example, Cichoń (1997) found that an organism being able to repair all current damage may decide to not repair them when the environment is risky or when the repair efficiency is not sufficient. In *L. sponsa* the seasonal constraints select for a rapid growth and development, and therefor indirectly result into a lowered investment into body maintenance and repair. The lack of full repair is likely to

Table 3
Maximum likelihood estimates (MLEs) and their confidence intervals for the best fitted model (**A**) per latitude, and (**B**) for the early and late cohorts at the south latitude.

Group	Model		*a*		*b*		γ		*c*	
A)										
N, age	GG	MLE	−7.03		0.1058		7.11		0	
		CI (LO,HI)	−7.81	−6.25	0.0653	0.1462	3.51	10.71	N/A	N/A
C, age	GGM	MLE	−19.63		0.1650		13.31		0.0039	
		CI (LO,HI)	−37.21	−2.04	−0.0471	0.3771	−19.84	46.45	0.0031	0.0046
S, age	GM	MLE	−8.19		0.0459		0		0.0014	
		CI (LO,HI)	−9.11	−7.27	0.0357	0.0561	N/A	N/A	0.0006	0.0023
N, degree-day	GG	MLE	−9.76		0.0051		6.98		0	
		CI (LO,HI)	−10.51	−9.02	0.0030	0.0073	3.25	10.71	N/A	N/A
C, degree-day	GGM	MLE	−28.37		0.0111		20.00		0.0002	
		CI (LO,HI)	−66.15	9.41	−0.0108	0.0330	−44.47	84.47	0.0002	0.0002
S, degree-day	GM	MLE	−11.41		0.0020		0		0.0001	
		CI (LO,HI)	−12.32	−10.49	0.0016	0.0025	N/A	N/A	0.0000	0.0001
N, light-day	GG	MLE	−6.83		0.0876		4.82		0	
		CI (LO,HI)	−7.63	−6.02	0.0439	0.1313	1.16	8.47	N/A	N/A
C, light-day	GGM	MLE	−16.50		0.1784		6.93		0.0050	
		CI (LO,HI)	−27.93	−5.08	−0.0016	0.3585	−8.37	22.22	0.0040	0.0060
S, light-day	GM	MLE	−8.20		0.0758		0		0.0024	
		CI (LO,HI)	−9.18	−7.21	0.0595	0.0920	N/A	N/A	0.0012	0.0037
B)										
S-early, age	GM	MLE	−8.60		0.0488		0		0.0021	
		CI (LO,HI)	−10.56	−6.64	0.0274	0.0703	N/A	N/A	0.0002	0.0039
S-late, age	GM	MLE	−8.68		0.0549		0		0.0035	
		CI (LO,HI)	−11.20	−6.16	0.0271	0.0827	N/A	N/A	0.0009	0.0061
S-early, degree-day	GM	MLE	−11.69		0.0022		0		0.0001	
		CI (LO,HI)	−13.50	−9.89	0.0013	0.0030	N/A	N/A	0.0000	0.0002
S-late, degree-day	GM	MLE	−12.13		0.0025		0		0.0002	
		CI (LO,HI)	−14.88	−9.39	0.0012	0.0037	N/A	N/A	0.0000	0.0003
S-early, light-day	GM	MLE	−8.78		0.0824		0		0.0035	
		CI (LO,HI)	−10.82	−6.75	0.0492	0.1157	N/A	N/A	0.0010	0.0060
S-late, light-day	GM	MLE	−8.57		0.0891		0		0.0054	
		CI (LO,HI)	−11.49	−5.65	0.0406	0.1377	N/A	N/A	0.0015	0.0093

Abbreviations as in Fig. 2.

Table 4
Result of likelihood ratio tests (LRT) comparing the parameters of the best fitted model (**A**) between latitudes and (**B**) between the early and late cohorts.

Comparison	Parameter	χ^2	df	p
A)				
N vs. S, age	a	3.24	1	0.0717
	b	9.06	1	0.0026
N vs. S, degree-days	a	6.52	1	0.0106
	b	9.05	1	0.0026
N vs. S, light-days	a	4.46	1	0.0348
	b	0.30	1	0.5851
B)				
S (early) vs. S (late), age	a	0.00	1	0.9625
	b	0.09	1	0.7610
	c	0.72	1	0.3961
S (early) vs. S (late), degree-days	a	0.08	1	0.7738
	b	0.13	1	0.7165
	c	0.74	1	0.3899
S (early) vs. S (late), light-days	a	0.01	1	0.9160
	b	0.04	1	0.8367
	c	0.61	1	0.4331

Comparisons northern vs. southern populations are made between models GG and GM and therefore only parameter a and b can be compared. Abbreviations as in Fig. 2.

lead to an increase in intrinsic mortality even before maturity and hence has the potential to lead to the here observed pattern that is consistent with pre-reproductive senescence. Consequently, we hypothesize that direct selection for rapid growth could indirectly cause senescence before reproduction.

One physiological factor that may cause senescence in early life is oxidative stress. According to theoretical models, faster growth rate is linked to a higher production of reactive oxygen species and thus may cause more oxidative damage (Mangel and Munch, 2005; Munch and Mangel, 2006). For example, in the congeneric damselfly *L. viridis*, rapid compensatory growth in the larval stage was associated with higher oxidative stress in the larval and adult stages (De Block and Stoks, 2008). Other costs of rapid growth and trade-offs between resources allocated to growth and other aspects of life, including repair, may occur. For example, resistance to free radicals can be negatively correlated with compensatory growth rate (Alonso-Alvarez et al., 2007). Accelerated growth in larvae of the damselfly *Ischnura elegans* was associated with reduced levels of the energetically costly stress protein Hsp70 (Stoks and De Block, 2011). In addition, Hsp70 participates in the regulation of somatic degeneration and thus may be involved in ageing (Minois et al., 2001; Tatar, 1999; Tatar et al., 1997).

4.2. Latitude- and cohort specific mortality patterns driven by time constraints

As predicted under higher time constraints, high-latitude larvae and late-hatched larvae had higher mortality rates. Moreover, high-latitude larvae also showed a higher rate of ageing (parameter *b*) compared to low-latitude larvae using both actuarial age and degree-days. Interestingly, the difference in ageing between latitudes was not observed when age was expressed in light-days. The photoperiod-based time scale measures the individual age as cumulated hours of day light experienced. If the photoperiod decreases through time than the rate of increase in light-days is slower. This suggests the importance of experienced light days in determining the pace of physiological processes connected with ageing. Theoretical models indicated that higher time constraints select for fast growth in order to reach maturity before the season ends, this comes at the cost of less allocation of energy to soma maintenance and repair (Kozłowski et al., 2004; Kozłowski and Wiegert, 1986). The higher time constraints thereby work in a similar way as additional extrinsic mortality and may increase the intrinsic mortality, and decrease the optimal age at maturity (Cichoń, 1997; Cichoń and Kozłowski, 2000) at the costs of smaller size (Kozłowski and Wiegert, 1986). An empirical support for a tradeoff between adult

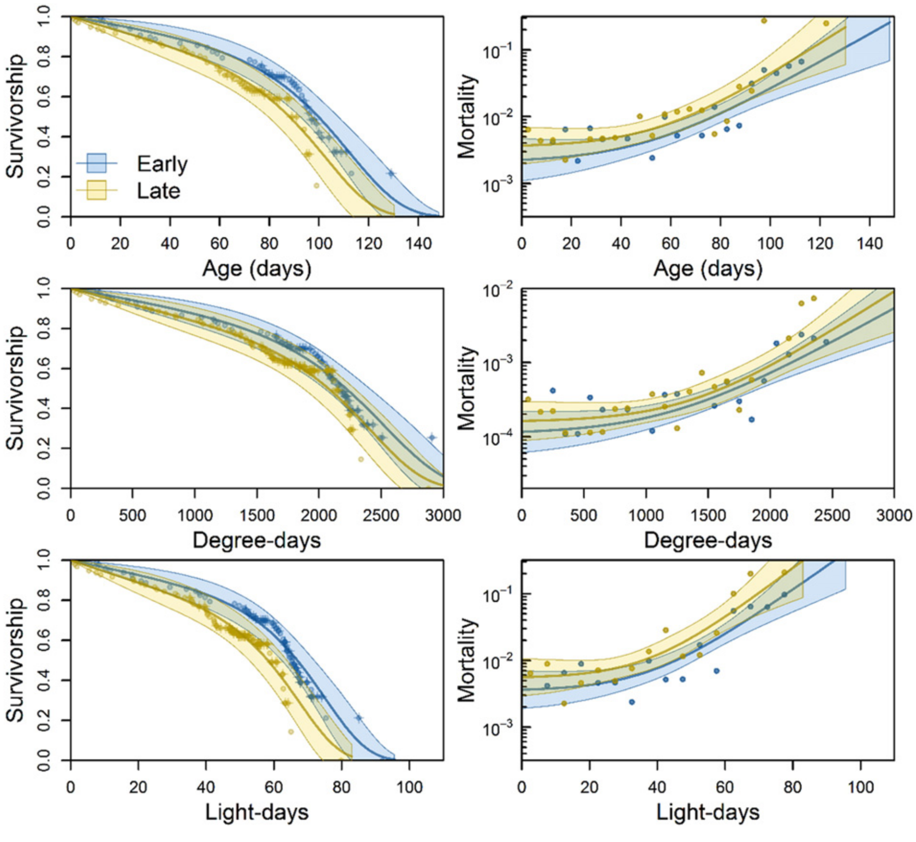

Fig. 3. Age-specific patterns in survivorship (left) and mortality rates (right) for the early and late cohorts of the southern (S) population.

size and rapid development imposed by time constraints associated with latitude was found in previous studies on *L. sponsa* (Sniegula et al., 2016c).

Individuals of a single homogenous population are likely to differ in their susceptibility to all causes of death, which is described as heterogeneity in frailty (Vaupel et al., 1979). When large enough this heterogeneity leads to observable bending down of the mortality curves at later ages, which was visible in N and C populations (Fig.2, see also S.III). We hypothesize that the higher time stress caused by a shorter season length in the N and C populations causes the higher heterogeneity in frailty. This is expected because under more stressful conditions even a small deviation from optimal allocation strategy has relatively bigger impact on mortality curves than in the less stressful conditions.

4.3. Conclusions

Little is known about latitudinal patterns of senescence and particularly about the occurrence and the mechanisms of pre-reproductive senescence. While some theories of ageing (Hamilton, 1966; Medawar, 1952) predict that senescence should start after maturity, in others that are based on trade-offs this is not a must (Cichoń, 1997). We found that *L. sponsa* exhibits accelerating larval mortality rates with age. This is consistent with a pattern of ageing as observed in adult animals (Pietrzak et al., 2015; Ricklefs and Scheuerlein, 2002) that is possibly driven by damage accumulation (Best, 2009; Tatar, 1999). The observed age-dependent increase in mortality rates was consistent across latitudes when reared under the natural temperature and photoperiod regimes as well as in common-garden experiment. We hypothesize that patterns consistent with pre-reproductive senescence may occur in other species facing high time constraints and with a long pre-reproductive life stage.

Authors contribution

S.S. initiated the project. M.J.D. and S.S. stated the hypotheses. S.S. planned the experiment, and S.S. and M.J.G. ran the experiments. M.J.D. analyzed and visualized the data. M.J.D and S.S. wrote the first draft that was further improved by R.S., A.D. and M.J.G. M.J.D, S.S., R.S., A.D., and M.J.G. wrote the final draft of the paper.

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Appendix A. Supplementary materials

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