

Warming and predation risk only weakly shape size-mediated priority effects in a cannibalistic damselfly

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Abstract

1. Differences in hatching dates can shape intraspecific interactions through size-mediated priority effects (SMPE), a phenomenon where bigger, early hatched individuals gain advantage over smaller, late hatched ones. While SMPE may be important for population dynamics, to what extent and how these are affected by key environmental factors such as warming and predation risk imposed by top predators remains unclear.
2. In a laboratory experiment, we studied effects of warming (low and high temperature) and predation risk (presence and absence of predator cues of perch) on SMPE in life history and physiological traits in the cannibalistic damselfly *Ischnura elegans*. We induced SMPE by manipulating hatching dates, thereby creating four groups: non-mixed phenology early (E) and late (L) hatchers, and mixed phenology early (E+L) and late (L+E) hatchers.
3. We found strong SMPE for survival and emergence success, with the highest values in E+L larvae and the lowest values in L+E larvae. Neither temperature nor predator cues affected SMPE for these two life history traits. The other life history traits (development rate and mass at emergence) did not show SMPE, but were affected by temperature and predator cues.
4. SMPE was found for protein content, but only in the high temperature treatment. The other physiological traits (immune function measured as phenoloxidase activity and fat content) showed fixed expressions across treatments, indicating decoupling between physiology and life history.
5. The results underline that SMPEs are trait-dependent, and only weakly affected by temperature and predation risk.

Introduction

One of the biggest challenges in ecology is to understand and predict the impact of climate change on species and populations (Blois et al. 2013; Merilä and Hendry 2014). However, such understanding is complicated by the fact that species are embedded in complex communities. Therefore, it is not enough to understand how species are affected by warming *per se*, but also how warming changes their antagonistic interactions (Yang and Rudolf 2010; Angert et al. 2013). Changes in temperature have indeed been shown to affect antagonistic interactions between organisms (Urban 2015; Ørsted et al. 2017; Grainger et al. 2018; Sniegula et al. 2019a). These changes in interactions can be caused by shifts in phenological events (Parmesan 2007), for example, in relative hatching dates of interactive organisms (Rudolf 2018; Carter and Rudolf 2019). In predator-prey systems, higher temperatures may lead to increased activity and encounter rates that benefits predators in terms of higher food acquisition, earlier time at maturity and larger final size (Rasmussen et al. 2014; Bailey and Pol 2016).

Specifically for cannibalistic interactions, the outcome of intraspecific encounters is strongly determined by the difference in body size (Anholt 1994; Johansson and Crowley 2008; Takashina and Fiksen 2020),

and encounter rates and cannibalism rates increase under warming (Crumrine 2010; Op de Beeck et al. 2018). In such situations, larger individuals take advantage over smaller individuals leading to so called size-mediated priority effects, SMPE (Rasmussen et al. 2014). There is accumulating evidence that changes in phenological events such as relative hatching dates increase the magnitude of SMPE due to larger variation in relative body size of interacting animals (Murillo-Rincón et al. 2017; Sniegula et al. 2019a). Although the theoretical background of priority effects in a warming world is well understood (Yang and Rudolf 2010; Fukami 2015), to our knowledge there have been few empirical approaches that linked life history with physiology in the context of SMPE caused by temperature-mediated hatching dates (Jermacz et al. 2020; Raczyński et al. 2021).

Predator-prey interactions can have direct consumptive, and indirect non-consumptive effects. Consumptive predator effects lead to the direct death of prey through prey consumption, while non-consumptive predator effects may reduce prey fitness through behavioural and physiological changes (Peacor and Werner 2000; Stoks et al. 2005; Hermann and Landis 2017; Sniegula et al. 2019b). For example, non-consumptive predator effects caused by visual or chemical predator cues can lead to reduced prey activity and food intake (Jiménez-Cortés et al. 2012; Weissburg et al. 2014; Gehr et al. 2018; Zhang et al. 2019). Prey may also increase growth rate to escape gape-limited predators (Arnett and Kinnison 2017), but this often leads to costs in terms of decreased size at maturity (Bell et al. 2011) and reduced ability to neutralize free radicals (De Block and Stoks 2008; Lee et al. 2010). Non-consumptive predator effects can have equally or even more negative consequences on prey communities than consumptive effects (Preisser et al. 2005; Catalán et al. 2021). However, it is still unclear whether and how the non-consumptive predator effects impact SMPE in prey, especially when prey represent intermediate, cannibalistic predators in a food chain, and the predators are at the top of the food chain. Furthermore, presence of predator cues may change the effect of warming on prey life history, e.g., by reducing the growth rate in prey (Miller et al. 2014; Gjoni et al. 2020). This makes interaction of these two factors (temperature and predator cues) especially important in predicting the final outcome of the predator-prey interactions, hence also of SMPE.

Here, we studied combined direct (intraspecific SMPE) and indirect (cues of perch, a top predator in ponds) predator effects on life history and physiology in the cannibalistic damselfly *Ischnura elegans* (an intermediate predator in ponds). By combining direct and indirect predator effects with two thermal conditions simulating the current and the predicted increased temperature by 2100 we could assess how both predator-induced effects may change under future warming. We examined SMPE in larval and adult life history and physiological traits and whether non-consumptive top predator effects in combination with increased temperature experienced during damselfly egg and larval stages affect SMPE. We had following set of hypotheses. (1) *I. elegans* shows SMPE in life history and physiological traits. We expected early hatchers to have advantage over late hatchers in terms of food acquisition, including cannibalism, leading early hatchers to show higher values for life history traits (survival, development rate and mass at emergence) and physiological traits (increased energy storage in a form of fat and protein content, and immune function measured as phenoloxidase activity) (Stoks et al. 2006b; Beckerman et al. 2010; Yang and Rudolf 2010; Lancaster et al. 2017; Sniegula et al. 2017b; Sniegula et al. 2019a). (2)

SMPE is more pronounced or more likely at the higher temperature as this leads to increased food acquisition through increased activity (Brown et al. 2004; Stoks et al. 2012; Wang et al. 2021; Pintanel et al. 2021), and more/earlier cannibalism (Op de Beeck et al. 2018, but see Sniegula et al., 2017a). (3) SMPE in life history and physiological traits is less pronounced when larvae experience additional stress imposed by top predator cues. *Ischnura* species show reduced activity and metabolic rate in the presence of fish predator cues (McPeck et al. 2001; Gyssels and Stoks 2006), which in turn might cause reduced food acquisition, including cannibalism, and decreased intensity of SMPE (Beermann et al., 2018; Schoener, 1971).

Methods

Study species and collection

In this experiment we used the damselfly *I. elegans* as focal species. As top predator, we used the European perch (*Perca fluviatilis*) to impose non-consumptive predator effects on the damselfly. *I. elegans* a common insect species in Europe, occurring from northern Spain to central Sweden (Dijkstra et al. 2020). Central Europe populations are uni- and bivoltine (one or two generations per year, respectively), depending on the thermal conditions (Corbet et al. 2006). Larvae hatch 2-3 weeks after egg laying. Eggs and larval stages commonly share habitats with predatory fish (Zwick 2001). Fish cues can affect egg and larval life histories and physiology in the study species (Stoks et al. 2015; Fontana-Bria et al., 2017; Sniegula et al., 2020).

Adult *I. elegans* females were collected at a pond in Zabierzów Bocheński, Poland (50°03'16.3"N, 20°19'45.7"E). This fish pond contains *P. fluviatilis*. In total, 40 and 36 females were caught in copula on 22 June 2019 (i.e., early group) and on 7 July 2019 (i.e., late group). Females were individually placed in plastic cups with perforated lids and wet filter paper for egg laying, and transported by car in a Styrofoam box to the Institute of Nature Conservation PAS (INC PAS), Krakow, Poland. Adult females were kept in a room at a temperature of 24°C and natural daylight (photoperiod). Females laid eggs within three days after they had been field-collected. In total 22 clutches were used for the early group treatment, and 26 clutches for the late group treatment. After egg laying, females were released in their natural population.

Ten *P. fluviatilis* (age: 1+) were caught in Dobczyce lake (49°52'27"N, 20°2'55"E) on 19 June 2019. Five fish were used in the experiment, another five were used as a backup. Fish collection and housing were done with a permission from the Local Ethical Committee (ref. 261/2019).

Housing

Egg clutches from early collected females were pooled, and the same was done with eggs from late collected females. The two hatching phenology groups, early (E) and late (L), had 16 days difference in hatching dates, corresponding to the time interval between adult damselfly field collection dates. Such difference in hatching dates occurs in the natural populations because of the long *I. elegans* mating season and mixed voltinism in the sampling region (Corbet et al. 2006; Mikolajczuk 2014). We also

created mixed phenology groups, where early hatched individuals shared the same container with late hatched individuals. Note that for the statistical analyses early and late hatched individuals in mixed phenology groups were considered as two different groups, E+L and L+E, where the group E+L referred to the early larvae in the presence of late larvae, and the group L+E to the late larvae in the presence of early larvae. This resulted in four phenology groups: non-mixed E and L, and mixed E+L and L+E. In the non-mixed phenology groups sets of 16 larvae of the same phenology group (E or L) were placed in separate containers, and in mixed phenology groups 8 larvae from E and 8 larvae from L phenology groups were placed in the same container, creating E+L and L+E phenology groups. This way all containers contained 16 larvae. Each phenology group was studied under the four combinations of two top predator treatments (fish predator cues present and absent) and two temperature treatments (22°C and 26°C, hereafter, low and high temperature). This created the following full factorial crossed design: 4 phenology groups × 2 predator cue treatments × 2 temperature treatments × 12 replicated containers × 16 larvae = 2304 individuals at the start (Fig. 1). Throughout the experiment we used a constant photoperiod of L:D 16:8h, which corresponds to the summer photoperiod, i.e., peak of the larval growth season, at the collection site. We used two climate incubators (Pol-Eko ST 700) for damselfly rearing.

Hatching took place on 6 July 2020 (E group) and 22 July 2020 (L group) at the high temperature, and on 11 July 2020 (E group) and 27 July 2020 (L group) at the low temperature treatment. At hatching, we randomly chose 16 larvae from E and L groups and transferred them to separate containers (16 × 12 cm, height 8 cm) filled with 600 mL of dechlorinated tap water and two nylon net strips, providing hiding space for larvae and climbing structure during emergence. In E+L and L+E groups, we randomly choose 8 larvae from the E group and 16 days later added 8 larvae from the L group. Larvae were fed twice a day (morning and afternoon feeding) with *Artemia salina* nauplii. During the feeding, E and L groups received 10 portions/container (mean = 201.9 nauplii/portion, SD = 17.2). In mixed groups, early hatched larvae received five portions until late hatched larvae were introduced to the same containers. From this time, mixed phenology groups received 10 portions/container.

Every other day, 150 mL of water in every container was refilled with water containing predator cues or no predator cues. Earlier studies have shown that chemical cues of aquatic predators have an average half-life degradation time of ca. 36.5 h (Buskirk et al. 2014). Previous experiments on non-consumptive predator effects in damselfly larvae supported this (Sniegula et al. 2019b; Sniegula et al. 2020).

To distinguish early from late hatched individuals in E+L and L+E groups, we cut the tibia of either one left or one right middle leg. Individuals from E and L groups were marked the same way. The larvae were marked when 30 days old. This marking persists until emergence and does not impact the measured traits (Hagler and Jackson 2001; Sniegula et al. 2019a).

Freshly emerged individuals were individually transferred to a dry plastic cup and kept for 24 hours until the cuticle hardened. Next, damselflies were weighted and frozen at -80°C for physiology analyses. The experiment ended when the last damselfly larvae emerged.

Response variables

Life history

The survival was noted daily between hatching and emergence. Individuals that emerged with fully developed body and wing parts were considered to have emerged successfully. Larval development time was measured as the number of days between hatching and emergence. One day after emergence, damselfly wet mass was measured to the nearest 0.1 mg with the use of an electronic balance (Radwag AS.62). The growth rate was calculated as adult wet mass divided by the number of days between hatching and emergence.

Physiology

For physiological analyses, damselfly bodies without legs and wings were grinded with phosphate buffer solution (15 μL for each milligram of wet mass) and centrifuged at 10,000 g for 5 minutes at 4°C. All physiology analyses were done on homogenates.

The classical procedure for measuring total body fat in insects (Marsh and Weinstein 1966) was optimized for damselfly bodies. A volume of 8 μL homogenate was mixed with 56 μL 100% sulfuric acid, and heated for 20 minutes at 150°C. After cooling down, 64 μL Milli-Q-Water was added. Of this mixture, 30 μL was put in a well of a 384-well microliter plate, and absorbance was measured at 340 nm. The measurements were made on an Infinite M2000 (TECAN) plate reader. To convert absorbances into fat contents, the standard curve of glyceryl tripalmitate was used. The average of three technical replicates per sample was used in the statistical analyses.

Protein content (μg of protein/mg of body mass) was determined using the Bradford (1976) method. Of the homogenate, 1 μL was mixed with 160 μL of Milli-Q-Water and 40 μL of Bio-Rad Protein Dye. After five minutes of incubation at 25°C, the absorbance was measured at 595 nm and converted into protein contents using standard curves of bovine serum albumin. The measurements were repeated three times per sample, and the average values used for statistical analyses.

A modified version of the assay described in Stoks et al. (2006) was used for determining PO activity. Of the homogenate, 10 μL was mixed with 10 μL of phosphoric buffered saline and 5 μL of chymotrypsin. The mixture was put in wells of a 384-well microtiter plate. Afterwards, the samples were incubated for 5 minutes at room temperature. After incubation, the substrate L-DOPA (1.966 mg dihydroxyphenyl-L-alanine per 1 mL of PBS-buffer) was added and mixed with the samples. Immediately afterwards, the linear increase in absorbance was measured at 490 nm every 20 seconds for 30 minutes at 30°C. The PO activity was quantified as the slope of the reaction curve, and the average of two technical replicates was used for statistical analyses.

Statistical methods

All analyses were run using R 4.0.4. (R Development Core Team 2019). Generalized mixed models with a binomial distribution were used to separately analyse the survival and emergence success (*glmer* function in the lme4 package, Bates et al., 2015). The other life history traits (development time, wet mass

and growth rate) and the physiological traits (PO activity, fat and protein contents) were analysed using linear mixed models (*lmer* function in the *lme4* package, Bates et al., 2015). In all models, phenology group, top predator cue treatment, temperature treatment and sex were entered as fixed effects. Initially, models with all possible interactions were run. Interaction terms with $p > 0.1$ were removed from the final models. In all models, container nested within phenology groups were used as random variable. SMPE would be indicated by the pattern where the trait value in the E+L group would be statistically higher (survival, mass, growth rate, fat content, protein content and PO activity) or lower (development time) than in the other phenology groups. If a factor with more than two levels or any interaction term was found statistically significant, *post hoc* Tukey HSD tests (function *lsmeans*) were run to test pairwise between-level differences. Because of low number of surviving larvae in the L+E group, this group was excluded from all analyses, except for survival until emergence and emergence success.

Results

Life history

There was a SMPE in survival until emergence, with other factors (temperature, predator cues and sex) not affecting the magnitude of SMPE in this trait. Phenology affected survival until emergence (Fig. 2A, Table 1), with larvae from the E+L group showing the highest survival, and larvae from the L+E group showing the lowest survival (Fig. 2A, Table S1). None of the interaction terms were significant (Fig. 2A, Table 1). The average percentage of survival in E+L, E, L and L+E groups were 20.1%, 11.98%, 10.29% and 2.1%, respectively (percentages based on raw data). The pattern in SMPE in emergence success was the same as for survival until emergence (Fig. S1, Table 1 and Table S2). There was no SMPE pattern in the other life history traits (development time, adult mass and growth rate).

Table 1

Results from mixed models on life history and physiological traits. Final models included all fixed effects and interactions with p-values < 0.1, whereby p-values \leq 0.05 were considered significant. Except for the analysis of survival until emergence and emergence success, the L+E phenology group was excluded from analyses due to low sample size ($N \leq 2$).

Predictor	Df	χ^2	p
Survival until emergence			
Phenology	3	55.59	<0.001
Temperature	1	0.54	0.46
Sex	1	0.04	0.84
Predator cues	1	0.11	0.73
Emergence success			
Phenology	3	46.95	<0.001
Temperature	1	0.17	0.68
Sex	1	0.08	0.78
Predator cues	1	0.47	0.49
Development time			
Phenology	2	11.97	0.003
Temperature	1	110.24	<0.001
Sex	1	2.14	0.14
Predator cues	1	0.64	0.42
Mass at emergence			
Phenology	2	3.73	0.15
Temperature	1	53.82	<0.001
Sex	1	16.26	<0.001
Predator cues	1	0.01	0.91
Temperature \times predator cues	2	7.75	0.02
Growth rate			
Phenology	2	22.79	<0.001
Temperature	1	63.1	<0.001

Predictor	Df	χ^2	p
Sex	1	0.72	0.4
Predator cues	1	0.78	0.38
Temperature × predator cues	2	5.12	0.08
Phenoloxidase activity			
Phenology	2	1.094	0.579
Temperature	1	1.434	0.231
Sex	1	0.01	0.922
Predator cues	1	0.913	0.339
Fat content			
Phenology	2	0.093	0.955
Temperature	1	0.796	0.231
Sex	1	0.244	0.621
Predator cues	1	2.302	0.373
Protein content			
Phenology	2	1.444	0.486
Temperature	1	0.796	0.654
Sex	1	0.786	0.375
Predator cues	1	0.097	0.755
Phenology × temperature	2	5.221	0.074
Phenology × sex	2	4.943	0.084

The phenology treatment had a significant effect on development time (Table 1), with larvae from E and E+L groups taking shorter time for development than larvae from the L group (Fig. 1B, Table S4). Development time was shorter at the high than at the low temperature (Fig. 1B, Table S4). Predator cues and sex had no effect on development time (Fig. 2b. Table 1).

The phenology treatment did not affect adult mass (Fig. 2C, Table 1). Larvae reared at the low temperature emerged at a higher mass than larvae reared at the high temperature (Fig. 2C, Tables 1 and Table S5). Predator cues increased the temperature effect on mass (temperature × predator cue interaction, Fig. 2 and Fig. S2, Table S5). Females had a higher mass than males (Tables 1, Table S5, Fig. S3).

The phenology affected the growth rate (Fig. 2D, Table 1). Larvae from E and E+L groups had higher growth rates than larvae from the L group (Fig. 2D, Tables 1 and Table S6). Larvae grew faster at the high temperature (Fig. 2D, Tables 1, Table S6). Predator cues tended to decrease the effect of temperature on growth rate (temperature \times predator cue interaction, $P = 0.08$, Fig. 2D, Fig. S4, Table 1, Table S6). Sexes did not differ in growth rate (Table 1).

Physiological traits

There were no SMPE patterns in phenoloxidase (PO) activity, fat content and protein content. None of the factors affected PO activity, fat content and protein content (Fig. 3A-C, Table 1). However, two interaction terms for protein content showed a trend. The high temperature tended to increase the phenology effect, with the E+L group reared at the high temperature having the highest protein content (phenology \times temperature interaction, Fig. 3C, Fig S5, Table 1), indicating SMPE at the high temperature. Males in the L group had a higher protein content than females, while the opposite pattern was present in the E group (phenology \times sex, Fig S9, Table 1). These interaction terms were not supported by the post-hoc tests (Table S9).

Discussion

We found a SMPE for two life history traits (survival until emergence and emergence success) that was similar across both temperatures supporting the first hypothesis, but not the second hypothesis. In addition, we detected a trend for SMPE for one physiological trait (protein content) but only at the high temperature matching our second hypothesis. Expression of other life history traits were in most cases affected by warming and predator cues, but for these traits we did not find SMPEs. The other physiological traits that we quantified showed fixed expressions across treatments, indicating that life history and physiological traits were to some extent decoupled in the study system.

Consistent with SMPE patterns, survival and emergence success were highest in larvae in the E+L group and lowest in those of the L+E group. These results support previous ones (Anholt 1994; Jara 2014; Cyrus et al. 2015; Sniegula et al. 2019a; Raczynski et al. 2021) and confirm that cannibalism benefits larger individuals. Contrary to the second and third prediction, neither temperature nor predator cues affected the strength of SMPEs in survival and emergence success. We suggest that the impact of these two factors were offset by larval antagonistic interactions. Antagonistic interactions can change larval behavior to avoid predation (Hermann and Landis 2017). Previous studies showed that life history traits in damselflies are altered by non-consumptive predator stress (Johansson et al. 2001; Stoks et al. 2012; Mikolajewski et al. 2015; Sniegula et al. 2019b; Sniegula et al. 2020; Antoł and Sniegula 2021) and temperature (Hassall and Thompson, 2008; for the study species: Debecker and Stoks, 2019; Stoks et al., 2012). But in these studies, the focus was on predator stress on damselfly egg stage or larval stage, but in the later case larvae were reared individually, thereby precluding cannibalism. Our current results add that SMPEs in key life history traits can affect population size, but that the strength of SMPEs is weakly altered by other environmental factors.

Despite the highest survival until successful emergence of E+L individuals, we did not detect SMPE in development rate. This result does not support previous results in other ectotherms, including the damselfly *L. sponsa*, which showed SMPE in development time as well as in other life history traits (Anderson and Semlitsch 2016; Sniegula et al. 2019a; Carter and Rudolf 2019). In the case of *L. sponsa*, early larvae from mixed groups had the shortest development times (Sniegula et al. 2019a). Therefore, we suggest that the differences could be caused by different life cycle characteristics. *L. sponsa* overwinters in the egg stage and is a strictly univoltine damselfly, while *I. elegans* overwinters in the larval stage and has a variable voltinism – a uni- and bivoltine damselfly in the study region (Corbet et al. 2006; Mikolajczuk 2014). These life cycle characteristics influence larval behavior, life history and physiology (Norling 2021). As species under high time constraints usually grow and develop faster (Abrams et al. 1996; Arendt 1997), a strictly univoltine species, *L. sponsa*, due to its short larval period after wintering in the egg stage is under higher growth pressure compared to univoltine *I. elegans*, which spends winter in the larval stage. However, a fraction of the *I. elegans* population may complete a second generation within the season (this as a result of cohort splitting, resulting in univoltine and bivoltine fractions), hence proceeds for direct larval development and emergence with no overwintering stage, and therefore is likely more time constrained (but still less than egg-overwintering *L. sponsa*), than the larval overwintering univoltine fraction (Norling 2021). Hence, the bivoltine fraction is likely more prone for SMPE. In the experiment, all phenology groups reared at the high temperature finished their larval development and emerged within 100 days (Fig. 2B). This fits the time necessary for the bivoltine fraction to finish its second generation within a season, especially in high temperature conditions, as recorded in local populations of *I. elegans* (Mikolajczuk 2014; Bobrek 2021). More studies, preferably in (semi)natural thermo-photoperiod conditions, allowing larval direct development until emergence (bivoltine) and larval overwintering (univoltine) are needed to clarify the effect of within population variation in voltinism on SMPE in damselflies.

Early hatched *I. elegans* from both mixed- and non-mixed phenology groups had shorter development times than late hatching. Shorter development times in early hatching were accompanied with elevated growth rates, and this led early hatching to reach similar mass at emergence as late hatching. Hence, there was apparently no trade-off between age and mass at emergence, which is often reported in ectotherms (Dmitriew 2011; Śniegula et al. 2012; Angell et al. 2020; Johansson et al. 2021; Nilsson-Örtman and Rowe 2021), but see (Rohner and Moczek 2021). These plastic life history responses of early hatching may be adaptive. Early emerged individuals mature early in the season and have higher mating success than delayed ones (Rolff et al. 2006). Usually there is also a positive association between adult mass and components of mating success (Honěk 1993; Beukeboom 2018). Additionally, we did not notice mortality costs of fast development rate, which is often reported (Lee et al. 2013; Burraco et al. 2017; Daňko et al. 2017). Early emergence is likely adaptive by allowing the completion of an extra generation within a year (hence bivoltinism), especially when temperature conditions are permissive (Corbet et al., 2006; Kong et al., 2019 Mikolajczuk, 2014). We hypothesize that early season hatching is selected for in this insect, despite no experimental evidence for SMPE in life history traits other than survival and successful emergence.

We found ecologically important temperature effects on life history traits which did not show SMPEs. As expected, the high temperature decreased development time, and the shorter development time resulted in a lower mass at emergence. This elevated temperature-driven trade off was somewhat reduced by increased growth rates at the high temperature, yet, the increase of growth rate was not strong enough to fully compensate the shorter development time. A similar incomplete compensating mechanism under warming was shown in previous studies, including studies on damselflies (De Block and Stoks 2003) and is considered one major mechanism for the here observed temperature-size rule where animals get smaller at higher temperatures (Verberk et al. 2021).

It has been demonstrated that non-consumptive predator effects can change prey life history traits (Hermann and Landis 2017; Sheriff et al. 2020; Wirsing et al. 2021), and could therefore potentially weaken or remove SMPE in prey, by, for example, reduced foraging rate in prey due to predator avoidance (McCauley et al. 2011; Thaler et al. 2012; Palacios and McCormick 2021). Here we show that predator cues affected damselfly life history, but without having an effect on SMPEs. Specifically, predator cues reduced larval growth rate, leading to a lower mass at emergence, but only in the high temperature treatment (predator cue × temperature interaction for growth and mass). This suggests that the expected temperature rise will likely increase non-consumptive predator stress in *I. elegans*, with potentially negative fitness consequences. Similar results were shown in previous studies on other ectotherms (Miller et al. 2014; Gjoni et al. 2020), including a damselfly (Janssens et al. 2015). These results could be explained in a following way: predator stress increases physiological stress in prey, and more energy is allocated into costly defence mechanism rather than growth rate in prey (Hawlena and Schmitz 2010). Taken together, current and previous results indicate that warming temperature may magnify the effects of predator-induced stress in prey, but that the increased predation stress may not affect SMPEs in prey.

Increased temperature led to a SMPE in protein content, a fundamental body building component (Nation 2011). This matched our second prediction of SMPEs being stronger or more likely at the high temperature. SMPE may be more likely under warming because a higher metabolism allows faster and more pronounced reactions to interactions between organisms, as well as the latter being stronger in general (Rudolf and Singh 2013; Grainger et al. 2018). A higher investment into proteins can have positive effects on body condition during the larval stage (Lee et al. 2008; Wu et al. 2018), and as proteins make up an important part of the swim muscles in damselfly larvae, may contribute to a better predator escape performance. Furthermore, this may generate positive carry-over effects across metamorphosis in the adult stage. For instance, proteins play an important role in ensuring proper wing elasticity, and as building blocks of flight muscles and the exoskeleton (Bullard et al. 2006; Muthukrishnan et al. 2012; Mamat-Noorhidayah et al. 2018). Intriguingly, the increased protein content under warming was not traded off against a faster growth rate, as it happened in body mass. This suggests that the larvae invest more energy into proteins than into other traits shaping final body size. It would be interesting to study in detail into which tissues the early hatched individuals invested more in the context of SMPEs.

We did not detect SMPEs in immune function (PO activity) and energy storage (fat content). These traits had similar values across all experimental treatments, suggesting fixed responses. These results are

surprising because previous studies showed that PO activity and fat storage increased under warming, and decrease under predator pressure but, again, when larvae were reared individually (Stoks et al. 2006b; Van Dievel et al. 2017). That the physiological traits did not follow the SMPE hypothesis confirms previous results in *L. sponsa* (Raczyński et al. 2021). Yet, in the latter species trait values showed plastic responses when individuals were exposed to time stressed conditions: PO activity decreased and fat content increased (Raczyński et al. 2021). In the current experiment we did not impose time stress, but it would be interesting to study this stress on SMPE in *I. elegans* and link it with variable voltinism in this damselfly.

In summary, our results confirm that SMPEs caused by differences in hatching phenology are an important factor that by shaping survival and emergence success can promote early emergence of amphibious and cannibalistic organisms in a population. Other central findings of current study were that warming and non-consumptive effects imposed by a top predator did not affect SMPE for life history traits, yet warming did generate a SMPE for larval protein content that may adaptively carry over to the adult stage. In agreement with theory (Takashina and Fiksen 2020), and current results, we suggest that given the high tendency for larval cannibalism, SMPEs in *I. elegans* could lead to directional selection for early adult breeding.

Declarations

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Author Contributions

SS originally formulated the idea, acquired funding, supervised experiment and project. MR, SS, and RS conceived and designed experiment. MR and SS performed field work, experiment, and statistical analysis. MR performed physiology analysis. MR, SS, and RS wrote the manuscript.

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Conflicts of interests

The authors declare that they have no conflict of interests

Ethics approval

All animal experiments were approved by Local Ethical Committee in Krakow, Poland, reference number 261/2019

Consent to participate

Not applicable

Consent to publication

Not applicable

Availability of data and material

All data generated or analysed during this study are included in this published article [and its supplementary information files].

Code availability

Not applicable

Author's contributions

Mateusz Raczyński: Data curation (equal); Formal analysis (equal); Investigation (equal); Methodology (equal); Software (equal); Visualization (equal); Writing – original draft (equal); Writing – review and editing (equal). Robby Stoks: Formal analysis (supporting); Methodology (supporting); Software (equal); Writing – original draft (supporting); Writing – review and editing (supporting). Szymon Sniegula: Conceptualization (equal); Formal analysis (equal); Funding acquisition (equal); Investigation (equal); Methodology (equal); Project administration (equal); Resources (equal); Supervision (equal); Validation (equal); Visualization (equal); Writing – original draft (equal); Writing – review and editing (equal).

References

1. Abrams PA, Leimar O, Nylin S, Wiklund C (1996) The Effect of Flexible Growth Rates on Optimal Sizes and Development Times in a Seasonal Environment. *Am Nat* 147(3):381–395. <https://doi.org/10.1086/285857>
2. Anderson TL, Semlitsch RD (2016) Top predators and habitat complexity alter an intraguild predation module in pond communities. *J Anim Ecol* 85(2):548–558. <https://doi.org/10.1111/1365-2656.12462>
3. Angell CS, Oudin MJ, Rode NO, Mautz BS, Bonduriansky R, Rundle HD (2020) Development time mediates the effect of larval diet on ageing and mating success of male antler flies in the wild. *Proc Royal Soc B* 287(1938):20201876. <https://doi.org/10.1098/rspb.2020.1876>
4. Angert AL, LaDeau SL, Ostfeld RS (2013) Climate change and species interactions: ways forward. *Ann N Y Acad Sci* 1297(1):1–7. <https://doi.org/10.1111/nyas.12286>
5. Anholt BR (1994) Cannibalism and Early Instar Survival in a Larval Damselfly. *Oecologia* 99(1/2):60–65
6. Antoń A, Sniegula S (2021) Damselfly eggs alter their development rate in the presence of an invasive alien cue but not a native predator cue. *Ecol Evol* 11(14):9361–9369. <https://doi.org/10.1002/ece3.7729>

7. Arendt JD (1997) Adaptive Intrinsic Growth Rates: An Integration Across Taxa. *Q Rev Biol* 72(2):149–177
8. Arnett HA, Kinnison MT (2017) Predator-induced phenotypic plasticity of shape and behavior: parallel and unique patterns across sexes and species. *Curr Zool* 63(4):369–378. <https://doi.org/10.1093/cz/zow072>
9. Bailey LD, van de Pol M (2016) Tackling extremes: challenges for ecological and evolutionary research on extreme climatic events. *J Anim Ecol* 85(1):85–96. <https://doi.org/10.1111/1365-2656.12451>
10. Bates D, Mächler M, Bolker B, Walker S (2015) Fitting Linear Mixed-Effects Models Using lme4. *J Stat Softw* 67(1):1–48. <https://doi.org/10.18637/jss.v067.i01>
11. Beckerman AP, Rodgers GM, Dennis SR (2010) The reaction norm of size and age at maturity under multiple predator risk. *J Anim Ecol* 79(5):1069–1076. <https://doi.org/10.1111/j.1365-2656.2010.01703.x>
12. Beermann J, Boos K, Gutow L, Boersma M, Peralta AC (2018) Combined effects of predator cues and competition define habitat choice and food consumption of amphipod mesograzers. *Oecologia* 186(3):645–654. <https://doi.org/10.1007/s00442-017-4056-4>
13. Bell AM, Dingemanse NJ, Hankison SJ, Langenhof MBW, Rollins K (2011) Early exposure to nonlethal predation risk by size-selective predators increases somatic growth and decreases size at adulthood in threespined sticklebacks. *J Evol Biol* 24(5):943–953. <https://doi.org/10.1111/j.1420-9101.2011.02247.x>
14. Beukeboom LW (2018) Size matters in insects – an introduction. *Entomol Exp Appl* 166(1):2–3. <https://doi.org/10.1111/eea.12646>
15. Blois JL, Zarnetske PL, Fitzpatrick MC, Finnegan S (2013) Climate Change and the Past, Present, and Future of Biotic Interactions. *Science* 341(6145):499–504. <https://doi.org/10.1126/science.1237184>
16. Bobrek R (2021) Odonate phenology recorded in a Central European location in an extremely warm season. *Biologia* 76(10):2957–2964. <https://doi.org/10.1007/s11756-021-00785-y>
17. Bradford MM (1976) A rapid and sensitive method for the quantitation of microgram quantities of protein utilizing the principle of protein-dye binding. *Anal Biochem* 72(1):248–254. [https://doi.org/10.1016/0003-2697\(76\)90527-3](https://doi.org/10.1016/0003-2697(76)90527-3)
18. Brown JH, Gillooly JF, Allen AP, Savage VM, West GB (2004) Toward a Metabolic Theory of Ecology. *Ecology* 85(7):1771–1789. <https://doi.org/10.1890/03-9000>
19. Bullard B, Garcia T, Benes V, Leake MC, Linke WA, Oberhauser AF (2006) The molecular elasticity of the insect flight muscle proteins projectin and kettin. *PNAS* 103(12):4451–4456. <https://doi.org/10.1073/pnas.0509016103>
20. Burraco P, Díaz-Paniagua C, Gomez-Mestre I (2017) Different effects of accelerated development and enhanced growth on oxidative stress and telomere shortening in amphibian larvae. *Sci Rep* 7:7494. <https://doi.org/10.1038/s41598-017-07201-z>

21. Buskirk JV, Krügel A, Kunz J, Miss F, Stamm A (2014) The Rate of Degradation of Chemical Cues Indicating Predation Risk: An Experiment and Review. *Ethology* 120(9):942–949. <https://doi.org/10.1111/eth.12266>
22. Carter SK, Rudolf VHW (2019) Shifts in phenological mean and synchrony interact to shape competitive outcomes. *Ecology* 100(11):e02826. <https://doi.org/10.1002/ecy.2826>
23. Catalán AM, Büchner-Miranda J, Riedemann B, Chaparro OR, Valdivia N, Scrosati RA (2021) Community-wide consequences of nonconsumptive predator effects on a foundation species. *J Anim Ecol* 90(5):1307–1316. <https://doi.org/10.1111/1365-2656.13455>
24. Corbet PS, Suhling F, Soendgerath D (2006) Voltinism of Odonata: a review. *Int J Odonatol* 9(1):1–44. <https://doi.org/10.1080/13887890.2006.9748261>
25. Crumrine PW (2010) Body size, temperature, and seasonal differences in size structure influence the occurrence of cannibalism in larvae of the migratory dragonfly, *Anax junius*. *Aquat Ecol* 44(4):761–770. <https://doi.org/10.1007/s10452-010-9314-z>
26. Cyrus AZ, Swiggs J, Santidrian Tomillo P, Paladino FV, Peters WS (2015) Cannibalism causes size-dependent intraspecific predation pressure but does not trigger autotomy in the intertidal gastropod *Agaronia propatula*. *J Molluscan Stud* 81(3):388–396. <https://doi.org/10.1093/mollus/eyv007>
27. Daňko MJ, Daňko A, Golab MJ, Stoks R, Sniegula S (2017) Latitudinal and age-specific patterns of larval mortality in the damselfly *Lestes sponsa*: Senescence before maturity? *Exp Gerontol* 95:107–115. <https://doi.org/10.1016/j.exger.2017.05.008>
28. De Block M, Stoks R (2003) Adaptive sex-specific life history plasticity to temperature and photoperiod in a damselfly. *J Evol Biol* 16(5):986–995. <https://doi.org/10.1046/j.1420-9101.2003.00581.x>
29. De Block M, Stoks R (2008) Compensatory growth and oxidative stress in a damselfly. *Proc Royal Soc B* 275(1636):781–785. <https://doi.org/10.1098/rspb.2007.1515>
30. Debecker S, Stoks R (2019) Pace of life syndrome under warming and pollution: integrating life history, behavior, and physiology across latitudes. *Ecol Monogr* 89(1):e01332. <https://doi.org/10.1002/ecm.1332>
31. Dijkstra K, Schröter A, Lewington R (2020) *Field Guide to the Dragonflies of Britain and Europe*. Second edition. Bloomsbury Publishing, London
32. Dmitriew CM (2011) The evolution of growth trajectories: what limits growth rate? *Biol Rev* 86(1):97–116. <https://doi.org/10.1111/j.1469-185X.2010.00136.x>
33. Fontana-Bria L, Selfa J, Tur C, Frago E (2017) Early exposure to predation risk carries over metamorphosis in two distantly related freshwater insects. *Ecol Entomol* 42(3):255–262. <https://doi.org/10.1111/een.12382>
34. Fukami T (2015) Historical Contingency in Community Assembly: Integrating Niches, Species Pools, and Priority Effects. *Annu Rev Ecol Evol Syst* 46(1):1–23. <https://doi.org/10.1146/annurev-ecolsys-110411-160340>

35. Gehr B, Hofer EJ, Ryser A, Vimercati E, Vogt K, Keller LF (2018) Evidence for nonconsumptive effects from a large predator in an ungulate prey? *Behav Ecol* 29(3):724–735.
<https://doi.org/10.1093/beheco/ary031>
36. Gjoni V, Basset A, Glazier DS (2020) Temperature and predator cues interactively affect ontogenetic metabolic scaling of aquatic amphipods. *Biol Lett* 16(7):20200267.
<https://doi.org/10.1098/rsbl.2020.0267>
37. Grainger TN, Rego AI, Gilbert B (2018) Temperature-Dependent Species Interactions Shape Priority Effects and the Persistence of Unequal Competitors. *Am Nat* 191(2):197–209.
<https://doi.org/10.1086/695688>
38. Gyssels F, Stoks R (2006) Behavioral responses to fish kairomones and autotomy in a damselfly. *J Ethol* 24(1):79–83. <https://doi.org/10.1007/s10164-005-0165-3>
39. Hagler JR, Jackson CG (2001) Methods for Marking Insects: Current Techniques and Future Prospects. *Annu Rev Entomol* 46(1):511–543. <https://doi.org/10.1146/annurev.ento.46.1.511>
40. Hassall C, Thompson DJ (2008) The effects of environmental warming on Odonata: a review. *Int J Odonatol* 11(2):131–153. <https://doi.org/10.1080/13887890.2008.9748319>
41. Hawlena D, Schmitz OJ (2010) Physiological stress as a fundamental mechanism linking predation to ecosystem functioning. *Am Nat* 176(5):537–556. <https://doi.org/10.1086/656495>
42. Hermann SL, Landis DA (2017) Scaling up our understanding of non-consumptive effects in insect systems. *Curr Opin Insect Sci* 20:54–60. <https://doi.org/10.1016/j.cois.2017.03.010>
43. Honěk A (1993) Intraspecific Variation in Body Size and Fecundity in Insects: A General Relationship. *Oikos* 66(3):483–492. <https://doi.org/10.2307/3544943>
44. Janssens L, Van Dievel M, Stoks R (2015) Warming reinforces nonconsumptive predator effects on prey growth, physiology, and body stoichiometry. *Ecology* 96(12):3270–3280.
<https://doi.org/10.1890/15-0030.1>
45. Jara FG (2014) Trophic ontogenetic shifts of the dragonfly *Rhionaeschna variegata*: the role of larvae as predators and prey in Andean wetland communities. *Ann Limnol* 50(2):173–184.
<https://doi.org/10.1051/limn/2014010>
46. Jermacz Ł, Kletkiewicz H, Nowakowska A, Dzierżyńska-Białończyk A, Klimiuk M, Kobak J (2020) Continuity of chronic predation risk determines changes in prey physiology. *Sci Rep* 10(1):6972.
<https://doi.org/10.1038/s41598-020-64000-9>
47. Jiménez-Cortés JG, Serrano-Meneses MA, Córdoba-Aguilar A (2012) The effects of food shortage during larval development on adult body size, body mass, physiology and developmental time in a tropical damselfly. *J Insect Physiol* 58(3):318–326. <https://doi.org/10.1016/j.jinsphys.2011.11.004>
48. Johansson F, Crowley PH (2008) Larval cannibalism and population dynamics of dragonflies. In: Lancaster J, Briers RA (eds) *Aquatic insects: challenges to populations*. CABI, Wallingford, pp 36–54
49. Johansson F, Stoks R, Rowe L, De Block M (2001) Life History Plasticity in a Damselfly: Effects of Combined Time and Biotic Constraints. *Ecology* 82(7):1857–1869. [https://doi.org/10.1890/0012-9658\(2001\)082\[1857:LHPIAD\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2001)082[1857:LHPIAD]2.0.CO;2)

50. Johansson F, Watts PC, Sniegula S, Berger D (2021) Natural selection mediated by seasonal time constraints increases the alignment between evolvability and developmental plasticity. *Evolution* 75(2):464–475. <https://doi.org/10.1111/evo.14147>
51. Kong JD, Hoffmann AA, Kearney MR (2019) Linking thermal adaptation and life-history theory explains latitudinal patterns of voltinism. *Philos Trans R Soc Lond B Biol Sci* 374(1778):20180547. <https://doi.org/10.1098/rstb.2018.0547>
52. Lancaster LT, Morrison G, Fitt RN (2017) Life history trade-offs, the intensity of competition, and coexistence in novel and evolving communities under climate change. *Philos Trans R Soc Lond B Biol Sci* 372(1712):20160046. <https://doi.org/10.1098/rstb.2016.0046>
53. Lee KP, Simpson SJ, Wilson K (2008) Dietary protein-quality influences melanization and immune function in an insect. *Funct Ecol* 22(6):1052–1061. <https://doi.org/10.1111/j.1365-2435.2008.01459.x>
54. Lee W-S, Monaghan P, Metcalfe NB (2010) The trade-off between growth rate and locomotor performance varies with perceived time until breeding. *J Exp Biol* 213(19):3289–3298. <https://doi.org/10.1242/jeb.043083>
55. Lee W-S, Monaghan P, Metcalfe NB (2013) Experimental demonstration of the growth rate–lifespan trade-off. *Proc Royal Soc B* 280(1752):20122370. <https://doi.org/10.1098/rspb.2012.2370>
56. Mamat-Noorhidayah, Yazawa K, Numata K, Norma-Rashid Y (2018) Morphological and mechanical properties of flexible resilin joints on damselfly wings (*Rhinocypha* spp.). *PLoS ONE* 13(3):e0193147. <https://doi.org/10.1371/journal.pone.0193147>
57. Marsh JB, Weinstein DB (1966) Simple charring method for determination of lipids. *J Lipid Res* 7(4):574–576
58. McCauley SJ, Rowe L, Fortin M-J (2011) The deadly effects of “nonlethal” predators. *Ecology* 92(11):2043–2048. <https://doi.org/10.1890/11-0455.1>
59. McPeck MA, Grace M, Richardson JML (2001) Physiological and Behavioral Responses to Predators Shape the Growth/Predation Risk Trade-Off in Damselflies. *Ecology* 82(6):1535–1545. <https://doi.org/10.2307/2679798>
60. Merilä J, Hendry AP (2014) Climate change, adaptation, and phenotypic plasticity: the problem and the evidence. *Evol Appl* 7(1):1–14. <https://doi.org/10.1111/eva.12137>
61. Mikolajczuk P (2014) Stwierdzenie wylotu drugiej generacji tężnicy małej *Ischnura pumilio* (Charpentier, 1825) i tężnicy wytwornej *Ischnura elegans* (Vander Linden, 1820) (Odonata: Coenagrionidae) w Polsce środkowo-wschodniej. *Odonatrix* 1(10)
62. Mikolajewski DJ, Conrad A, Joop G (2015) Behaviour and body size: plasticity and genotypic diversity in larval *Ischnura elegans* as a response to predators (Odonata: Coenagrionidae). *Int J Odonatol* 18(1):31–44. <https://doi.org/10.1080/13887890.2015.1012653>
63. Miller LP, Matassa CM, Trussell GC (2014) Climate change enhances the negative effects of predation risk on an intermediate consumer. *Glob Chang Biol* 20(12):3834–3844. <https://doi.org/10.1111/gcb.12639>

64. Murillo-Rincón AP, Kolter NA, Laurila A, Orizaola G (2017) Intraspecific priority effects modify compensatory responses to changes in hatching phenology in an amphibian. *J Anim Ecol* 86(1):128–135. <https://doi.org/10.1111/1365-2656.12605>
65. Muthukrishnan S, Merzendorfer H, Arakane Y, Kramer KJ (2012) 7 - Chitin Metabolism in Insects. In: Gilbert LI (ed) *Insect Molecular Biology and Biochemistry*. Academic Press, San Diego, pp 193–235
66. Nation JL (2011) *Insect Physiology and Biochemistry*, 2nd edn. CRC Press, Boca Raton
67. Nilsson-Örtman V, Rowe L (2021) The evolution of developmental thresholds and reaction norms for age and size at maturity. *PNAS* 118(7). <https://doi.org/10.1073/pnas.2017185118>
68. Norling U (2021) Growth, winter preparations and timing of emergence in temperate zone odonata: Control by a succession of larval response patterns. *Int J Odonatol* 24:1–36
69. Op de Beeck L, Verheyen J, Stoks R (2018) Competition magnifies the impact of a pesticide in a warming world by reducing heat tolerance and increasing autotomy. *Environ Pollut* 233:226–234. <https://doi.org/10.1016/j.envpol.2017.10.071>
70. Ørsted M, Schou MF, Kristensen TN (2017) Biotic and abiotic factors investigated in two *Drosophila* species – evidence of both negative and positive effects of interactions on performance. *Sci Rep* 7(1):40132. <https://doi.org/10.1038/srep40132>
71. Palacios M, del McCormick M MI (2021) Positive indirect effects of top-predators on the behaviour and survival of juvenile fishes. *Oikos* 130(2):219–230. <https://doi.org/10.1111/oik.07731>
72. Parmesan C (2007) Influences of species, latitudes and methodologies on estimates of phenological response to global warming. *Glob Chang Biol* 13(9):1860–1872. <https://doi.org/10.1111/j.1365-2486.2007.01404.x>
73. Peacor SD, Werner EE (2000) Predator Effects on an Assemblage of Consumers Through Induced Changes in Consumer Foraging Behavior. *Ecology* 81(7):1998–2010. [https://doi.org/10.1890/0012-9658\(2000\)081\[1998:PEOAAO\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2000)081[1998:PEOAAO]2.0.CO;2)
74. Pintanel P, Tejedo M, Salinas-Ivanenko S, Jervis P, Merino-Viteri A (2021) Predators like it hot: Thermal mismatch in a predator-prey system across an elevational tropical gradient. *J Anim Ecol*. <https://doi.org/10.1111/1365-2656.13516>
75. Preisser EL, Bolnick DI, Benard MF (2005) Scared to Death? The Effects of Intimidation and Consumption in Predator–Prey Interactions. *Ecology* 86(2):501–509. <https://doi.org/10.1890/04-0719>
76. R Development Core Team (2019) R: The R Project for Statistical Computing. In: Vienna, Austria. <https://www.r-project.org/>. Accessed 24 Mar 2021
77. Raczyński M, Stoks R, Johansson F, Sniegula S (2021) Size-mediated priority effects are trait-dependent and consistent across latitudes in a damselfly. *Oikos* 130(9):1535–1547. <https://doi.org/10.1111/oik.08353>
78. Rasmussen NL, Allen BGV, Rudolf VHW (2014) Linking phenological shifts to species interactions through size-mediated priority effects. *J Anim Ecol* 83(5):1206–1215. <https://doi.org/10.1111/1365-2656.12203>

79. Rohner PT, Moczek AP (2021) Evolutionary and plastic variation in larval growth and digestion reveal the complex underpinnings of size and age at maturation in dung beetles. *Ecol Evol* 11(21):15098–15110. <https://doi.org/10.1002/ece3.8192>
80. Rolff J, Fellowes M, Holloway G (2006) *Insect Evolutionary Ecology: Proceedings of the Royal Entomological Society's 22nd Symposium*. CABI Oxford University Press, Wallingford; Cary
81. Rudolf VHW (2018) Nonlinear effects of phenological shifts link interannual variation to species interactions. *J Anim Ecol* 87(5):1395–1406. <https://doi.org/10.1111/1365-2656.12850>
82. Rudolf VHW, Singh M (2013) Disentangling climate change effects on species interactions: effects of temperature, phenological shifts, and body size. *Oecologia* 173(3):1043–1052. <https://doi.org/10.1007/s00442-013-2675-y>
83. Schoener TW (1971) Theory of Feeding Strategies. *Annu Rev Ecol Evol Syst* 2(1):369–404. <https://doi.org/10.1146/annurev.es.02.110171.002101>
84. Sheriff MJ, Peacor SD, Hawlena D, Thaker M (2020) Non-consumptive predator effects on prey population size: A dearth of evidence. *J Anim Ecol* 89(6):1302–1316. <https://doi.org/10.1111/1365-2656.13213>
85. Sniegula S, Golab MJ, Johansson F (2019a) Size-mediated priority and temperature effects on intra-cohort competition and cannibalism in a damselfly. *J Anim Ecol* 88(4):637–648. <https://doi.org/10.1111/1365-2656.12947>
86. Sniegula S, Golab MJ, Johansson F (2017a) Cannibalism and activity rate in larval damselflies increase along a latitudinal gradient as a consequence of time constraints. *BMC Evol Biol* 17(1):167. <https://doi.org/10.1186/s12862-017-1010-3>
87. Sniegula S, Janssens L, Stoks R (2017b) Integrating multiple stressors across life stages and latitudes: Combined and delayed effects of an egg heat wave and larval pesticide exposure in a damselfly. *Aquat Toxicol* 186:113–122. <https://doi.org/10.1016/j.aquatox.2017.02.029>
88. Śniegula S, Johansson F, Nilsson-Örtman V (2012) Differentiation in developmental rate across geographic regions: a photoperiod driven latitude compensating mechanism? *Oikos* 121(7):1073–1082. <https://doi.org/10.1111/j.1600-0706.2011.20015.x>
89. Sniegula S, Nsanzimana J, d'Amour, Johansson F (2019b) Predation risk affects egg mortality and carry over effects in the larval stages in damselflies. *Freshw Biol* 64(4):778–786. <https://doi.org/10.1111/fwb.13261>
90. Sniegula S, Raczyński M, Golab MJ, Johansson F (2020) Effects of predator cues carry over from egg and larval stage to adult life-history traits in a damselfly. *Freshw Sci* 39(4):804–811. <https://doi.org/10.1086/711374>
91. Stoks R, Block MD, McPeck MA (2006a) Physiological Costs of Compensatory Growth in a Damselfly. *Ecology* 87(6):1566–1574. [https://doi.org/10.1890/0012-9658\(2006\)87\[1566:PCOCG\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2006)87[1566:PCOCG]2.0.CO;2)
92. Stoks R, Block MD, Meutter FVD, Johansson F (2005) Predation cost of rapid growth: behavioural coupling and physiological decoupling. *J Anim Ecol* 74(4):708–715. [Page 20/24](https://doi.org/10.1111/j.1365-</div><div data-bbox=)

93. Stoks R, Block MD, Slos S, Doorslaer WV, Rolff J (2006b) Time Constraints Mediate Predator-Induced Plasticity in Immune Function, Condition, and Life History. *Ecology* 87(4):809–815. [https://doi.org/10.1890/0012-9658\(2006\)87\[809:TCMPP\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2006)87[809:TCMPP]2.0.CO;2)
94. Stoks R, Swillen I, Block MD (2012) Behaviour and physiology shape the growth accelerations associated with predation risk, high temperatures and southern latitudes in *Ischnura damselfly* larvae. *J Anim Ecol* 81(5):1034–1040. <https://doi.org/10.1111/j.1365-2656.2012.01987.x>
95. Takashina N, Fiksen Ø (2020) Optimal reproductive phenology under size-dependent cannibalism. *Ecol Evol* 10(10):4241–4250. <https://doi.org/10.1002/ece3.6192>
96. Thaler JS, McArt SH, Kaplan I (2012) Compensatory mechanisms for ameliorating the fundamental trade-off between predator avoidance and foraging. *PNAS* 109(30):12075–12080. <https://doi.org/10.1073/pnas.1208070109>
97. Urban MC (2015) Accelerating extinction risk from climate change. *Science* 348(6234):571–573. <https://doi.org/10.1126/science.aaa4984>
98. Van Dievel M, Stoks R, Janssens L (2017) Beneficial effects of a heat wave: higher growth and immune components driven by a higher food intake. *J Exp Biol* 220(21):3908–3915. <https://doi.org/10.1242/jeb.158899>
99. Verberk WCEP, Atkinson D, Hoefnagel KN, Hirst AG, Horne CR, Siepel H (2021) Shrinking body sizes in response to warming: explanations for the temperature–size rule with special emphasis on the role of oxygen. *Biol Rev* 96(1):247–268. <https://doi.org/10.1111/brv.12653>
100. Wang Y-J, Sentis A, Tüzün N, Stoks R (2021) Thermal evolution ameliorates the long-term plastic effects of warming, temperature fluctuations and heat waves on predator–prey interaction strength. *Funct Ecol* 35(7):1538–1549. <https://doi.org/10.1111/1365-2435.13810>
101. Weissburg M, Smee DL, Ferner MC, Schmitz AEOJ, Bronstein EJJ (2014) The Sensory Ecology of Nonconsumptive Predator Effects. *Am Nat* 184(2):141–157. <https://doi.org/10.1086/676644>
102. Wirsing AJ, Heithaus MR, Brown JS, Kotler BP, Schmitz OJ (2021) The context dependence of non-consumptive predator effects. *Ecol Lett* 24(1):113–129. <https://doi.org/10.1111/ele.13614>
103. Wu Q, Patočka J, Kuča K (2018) Insect Antimicrobial Peptides, a Mini Review. *Toxins (Basel)* 10(11):461. <https://doi.org/10.3390/toxins10110461>
104. Yang LH, Rudolf VHW (2010) Phenology, ontogeny and the effects of climate change on the timing of species interactions. *Ecol Lett* 13(1):1–10. <https://doi.org/10.1111/j.1461-0248.2009.01402.x>
105. Zhang D-W, Xiao Z-J, Zeng B-P, Li K, Tang Y-L (2019) Insect Behavior and Physiological Adaptation Mechanisms Under Starvation Stress. *Front Physiol* 10:163. <https://doi.org/10.3389/fphys.2019.00163>
106. Zwick P (2001) CORBET, P.S. (1999): Dragonflies: Behaviour and Ecology of Odonata. *Aquat Insects* 23(1):83–83. <https://doi.org/10.1076/aqin.23.1.83.4929>

Figures

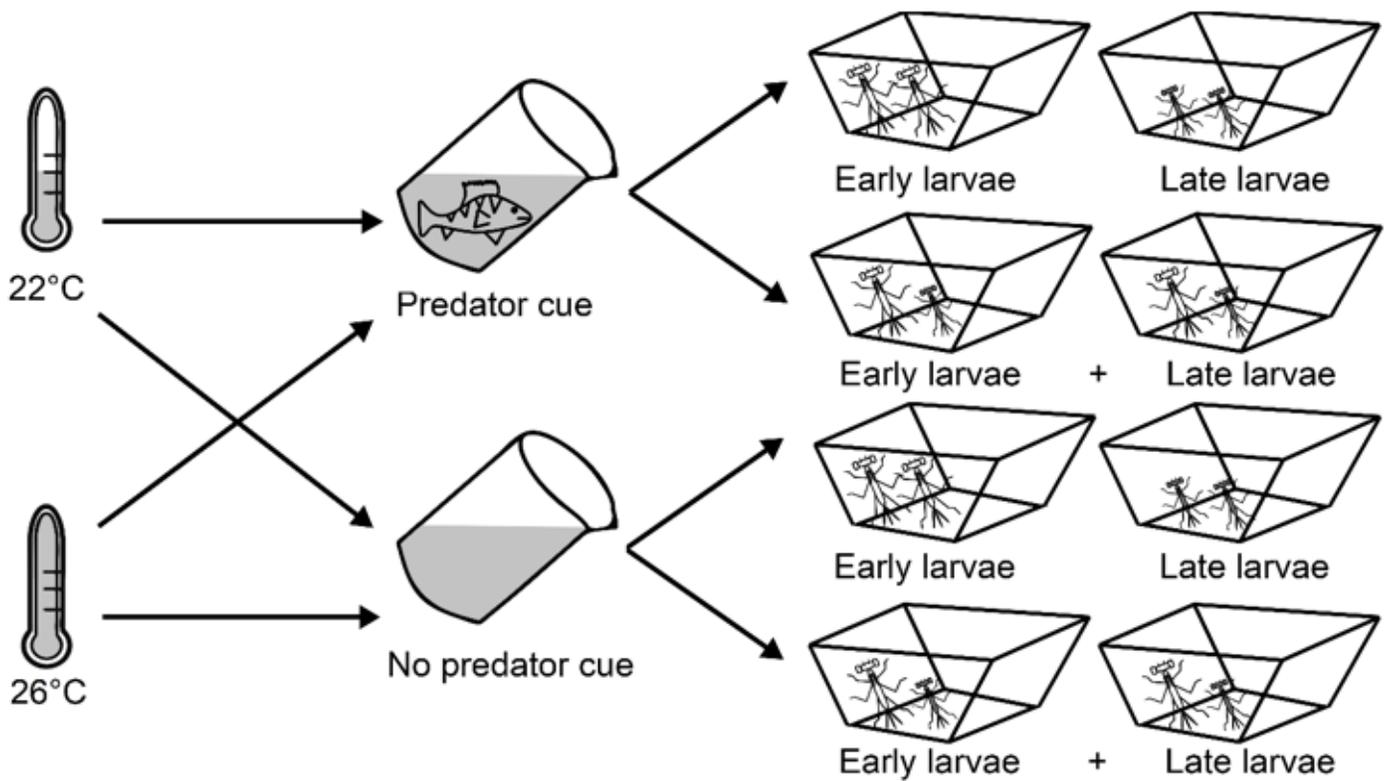


Figure 1

A schematic graph visualizing the full factorial experimental design with two temperature treatment groups crossed with two different predator cue treatment groups, that were each divided into four different phenology groups, resulting in 16 treatment combination groups. Note that in reality 16 larvae were present per container

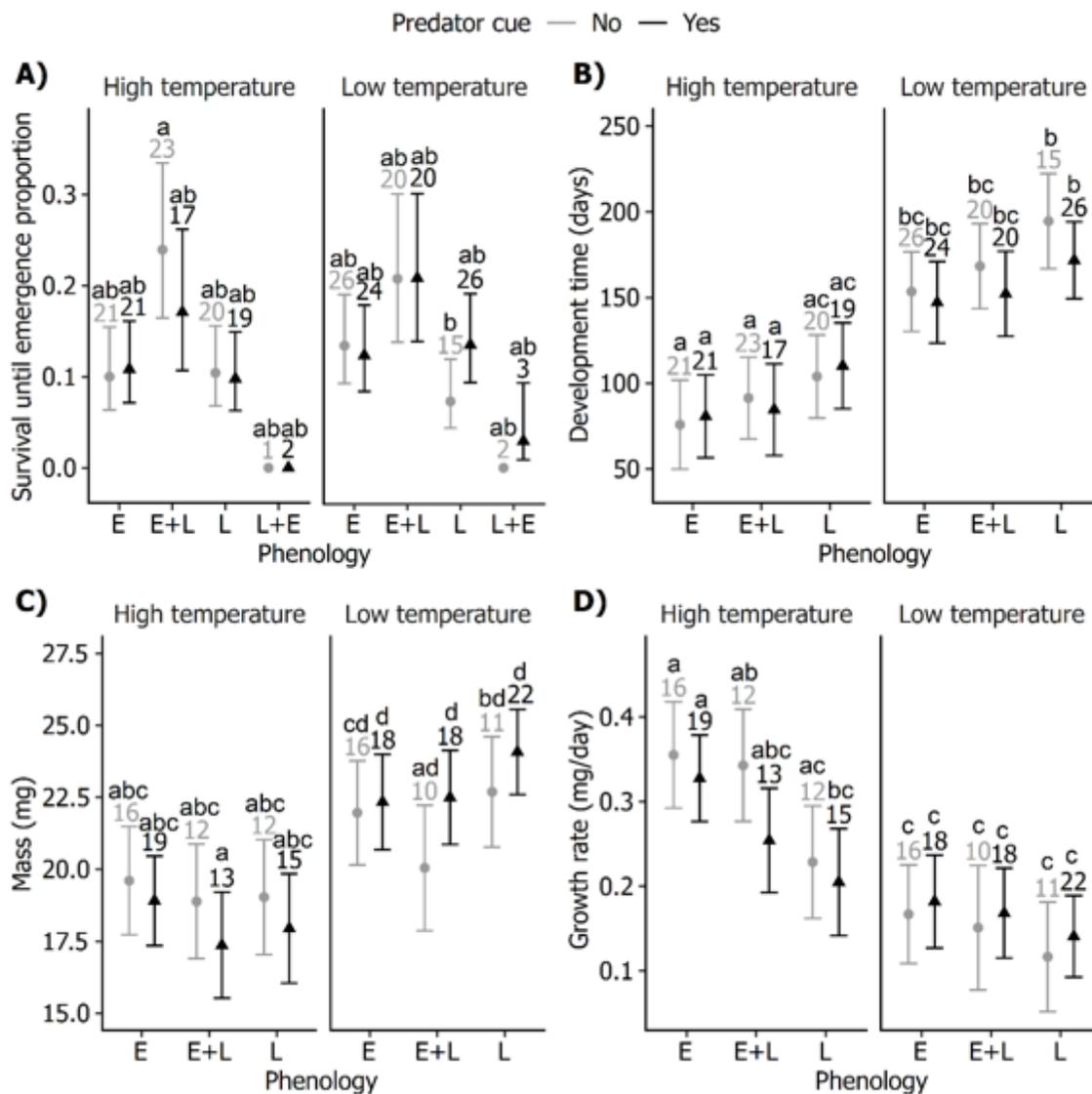


Figure 2

(A) Proportion of survival, (B) development time, (C) adult mass and (D) growth rate across different phenology groups (E, E+L, L and L+E), temperatures (high and low) and top predator cues (no and yes). Error bars indicate estimated 95% CI. The numbers on top of error bars represent the number of larvae within each group. E = early larvae, E+L = early larvae in mixed phenology group, L = late larvae, L+E = late larvae in mixed phenology group. Because of low sample sizes in the L+E phenology group, the L+E group was removed from all analyses, except for analysis on survival rate and emergence success. Letter codes indicate significant differences between phenology groups across both temperatures and predator cue treatments

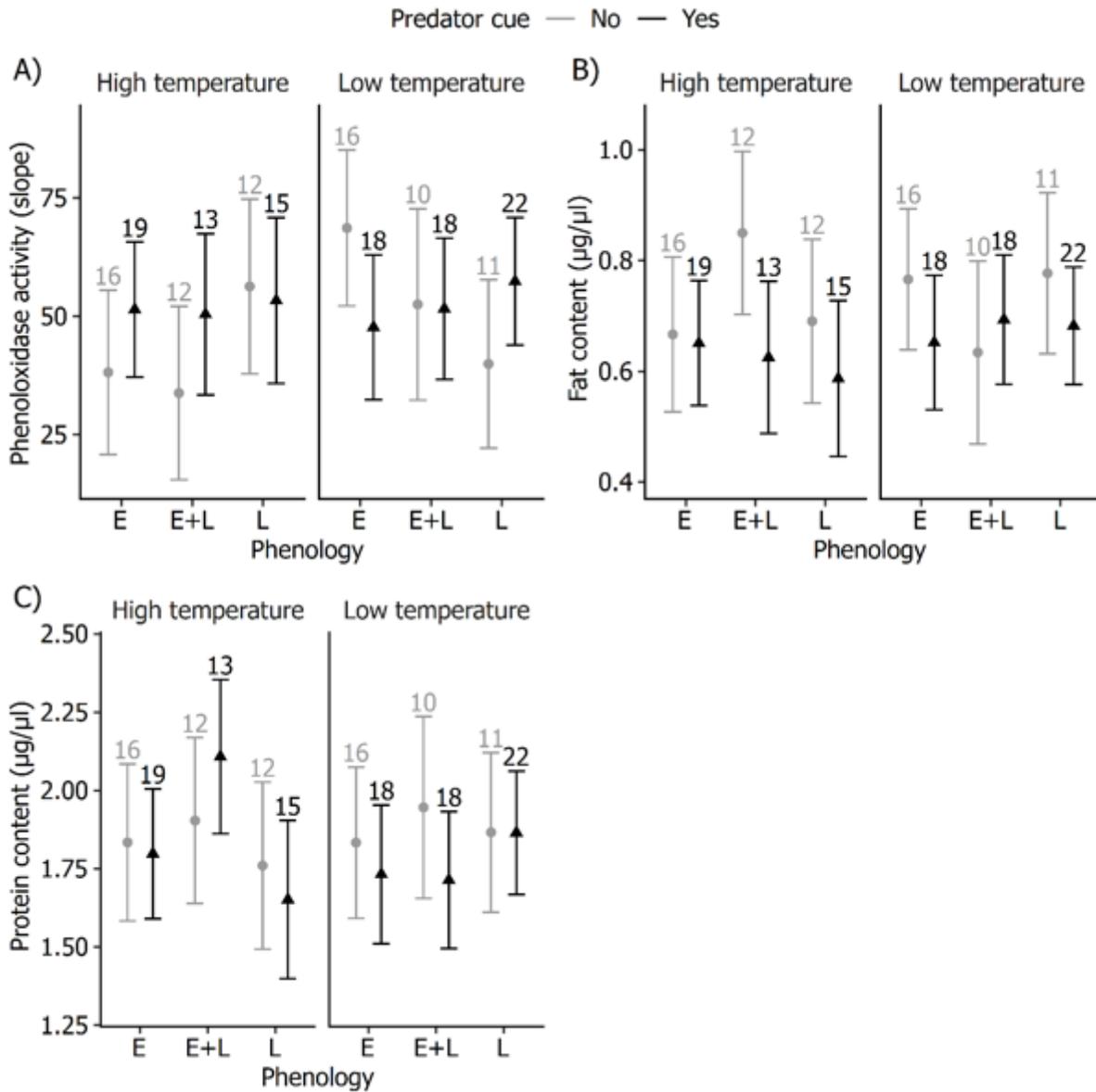


Figure 3

(A) Phenoloxidase activity, (B) fat content and (C) protein content, across different phenology groups (E, E+L and L), temperatures (high and low) and predator cues (no and yes). Error bars indicate estimated 95% CI. The numbers on top of error bars represent the number of larvae within each group. Letter codes were not added due to lack of support of statistically significant differences between groups from post-hoc tests. Abbreviations as in Fig. 2

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