Effects of predator cues carry over from egg and larval stage to adult life-history traits in a damselfly

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Abstract: Non-consumptive predator effects experienced in early life stages of prey may result in life-history costs in later life stages. Such effects can, for example, alter the growth rate during the juvenile stage, which may carry over to size at maturity. However, we have limited knowledge of the carry-over effects starting from the egg stage through the larval stage to the adult stage. Here, we present results from a laboratory experiment in which we exposed a damselfly, Ischnura elegans, to chemical cues originating from a fish predator, perch. We used a 2 x 2-full-factorial design in which the damselflies were exposed to predator cues during either the immobile egg or the mobile larval stage. The presence of predator cues, i.e., non-consumptive predator effects, during the egg stage caused decreased survival, but only until 2 wk after larval hatching. Predator cues during the larval stage caused decreased survival until emergence and an increase in development time until emergence. However, mass at emergence was not affected by predator cues. When fish cues were present in the egg or larval stage, there was a lower growth rate until final-instar larvae than in larvae that did not receive fish cues. Our results add to the growing number of studies showing that predation-risk cues in the egg stage can carry over to the adult stage, which ultimately could have consequences for adult life-history traits, such as survival and fecundity.

Key words: predator cue, carry-over effects, life history, kairomone, predator–prey interaction, phenotypic plasticity, complex life cycle

Indirect non-consumptive effects of predators on prey are defined as effects that do not kill the prey but incur costs, such as reduced feeding, a change in diet, or increased physiological stress (Peacor and Werner 2000, Stoks et al. 2005, Hawlena and Perez-Mellado 2009). Direct consumptive effects are defined as the killing of the prey. Indirect non-consumptive effects and direct consumptive effects are also referred to as trait-mediated and density-mediated effects, respectively (Abrams 2007). The costs of indirect non-consumptive effects usually have a negative effect on survival and reproduction (Zanette et al. 2003, Creel et al. 2009) and can thus have important consequences for population and community dynamics (Abrams 1995, Preisser et al. 2005). The impact of indirect non-consumptive effects can be as strong as or stronger than that of direct consumptive effects (Preisser et al. 2005). Information on how indirect non-consumptive processes affect survival, development, and size at maturation can thus provide an important mechanistic understanding of how these impacts may affect population dynamics.

Many organisms have complex life cycles, defined as ontogenetic changes in physiology, morphology, or behavior associated with a habitat shift (Wilbur 1980). For example, many aquatic insects start as eggs, following which they undergo an aquatic larval stage and then shift to a terrestrial stage during which maturation and mating occur. It is reasonable to assume that predation risk may differ among these 3 stages: egg, larva, and adult (Wilbur 1980). It is, therefore, interesting to examine whether the effects of exposure to non-consumptive predation risk carry over through these stages and to compare the strength of these effects between stages. Such studies are relevant because predation risk may vary across space and time during an organism’s ontogeny (Tolon et al. 2009).

Past studies have found strong carry-over effects between the larval stage and the adult stage in amphibians and insects. When exposed to predation cues (i.e., non-consumptive predation risk), these organisms usually show longer development times and a larger size at metamorphosis, although...
other patterns might occur (Ball and Baker 1996, Laurila et al. 1998, Benard 2004, Costanzo et al. 2011, Sniegula et al. 2019b). However, few studies have focused on how predation risk during the egg stage affects the later larval and adult stages and whether a switch from high predation risk to low predation risk over ontogeny can be compensated for in later ontogenetic stages. Nevertheless, prey can detect predator cues in the egg stage and show earlier or later hatching in response to predation risk during this stage (Warkentin 1995, 2011, Moore et al. 1996, Sniegula et al. 2019a).

Since eggs respond to non-lethal predation cues, it is interesting to examine how such cues affect later life-history stages. In one of the few studies that have explored how predation risk in the egg stage affects adult traits, Fontana-Bria et al. (2017) found that non-lethal predation cues from predatory damselfly larvae affected wing size but not adult size in a damselfly. They also found that the same cues caused longer development times until metamorphosis in females but not in males of a mosquito (Fontana-Bria et al. 2017). However, more studies are needed to explore the commonness of these carry-over effects from the egg stage into the adult stage.

Here, we examine how non-lethal predator cues experienced during the egg stage, larval stage, or both affect the survival, development, growth of larvae, and mass at emergence of the damselfly Ischnura elegans Vander Linden, 1820. We predicted that eggs or larvae exposed to predator fish cues would have lower survival until emergence, lower mass at emergence, and a longer development time until emergence in comparison to controls that did not experience such cues in the egg or larval stage. We based our predictions on the flexible growth and development time effort model in Abrams and Rowe (1996). However, many more scenarios for these life-history traits are possible (Abrams and Rowe 1996, Benard 2004).

**METHODS**

**Experimental design**

We used a laboratory experiment with a complete $2 \times 2$ design in which damselfly (*I. elegans*) eggs and larvae were sequentially exposed to fish cues or no fish cues (Fig. 1) to examine indirect non-consumptive effects of predator cues and assess how these effects influenced life-history traits in larval and adult stages.

We caught adult *I. elegans* females at Plaszów Pond, Poland (50°02′26″N, 19°58′15″E) on 20 July 2018 using standard methods (Sniegula et al. 2019a). The species has an aquatic egg and larval stage followed by a terrestrial adult stage. Eggs and larvae commonly share habitat with fishes (Corbet 1999, Le Gall et al. 2017, Sniegula et al. 2019a). Fishes present at Plaszów Pond include European Perch (*Perca fluviatilis* Linnaeus, 1758). We captured 15 female damselflies and placed them in individual plastic cups with wet filter paper for egg laying. Perforated lids that allow ventilation were put on the cups. Immediately after collection, we transported the cups by car to the Institute of Nature Conservation Polish Academy of Sciences, Kraków, Poland.

Upon arrival to the laboratory, we placed the cups with females in a room with natural light conditions at room temperature. Ten females laid eggs within the next 2 d. Thereafter, we released all females into the wild. Each clutch (family) contained hundreds of eggs, and we used 10 families for the experiment. We split each family into 2 halves, which we placed separately in plastic containers (15 × 10 × 6.5 cm) filled with 400 mL of dechlorinated aged tap water. We treated ½ of each clutch with perch cues as described below. We designated the other ½ as a control, which received no perch cues. On the day of hatching (8 August 2018), we divided the perch treatment group into 2 subgroups: the perch (egg)–perch (larval) treatment subgroup and the perch (egg)–no perch (larval) treatment subgroup.
We also divided the control group into 2 subgroups: the no perch (egg)–perch (larval) subgroup and the no perch (egg)–no perch (larval) treatment subgroup (Fig. 1).

At hatching, each treatment received 5 larvae from each family, i.e., 20 larvae/family were included in the experiment. Each treatment had 10 replicates (families); thus, there were 200 individuals at the start of the experiment. We randomly chose 5 individuals from each family and moved them to individual 200-mL plastic cups filled with 100 mL of aged tap water. The larvae shared the same cups for another 15 d to increase survival (De Block and Stoks 2003). Next, we placed the larvae individually in 200-mL plastic cups and treated ½ with perch cues and ½ without perch cues, the same way as during the first 15 d after hatching. Throughout the experiment, we fed larvae twice/d with nauplii of Artemia salina (mean = 201.8 nauplii/portion, standard error = 6.71 nauplii, n = 10 portions). After larvae entered the pre-final instar, we supplemented their diet with 3 standard-size Chironomidae larvae every Monday, Wednesday, and Friday.

**Predator-cue treatments**

To provide constant predatory cues for the perch treatment groups (Van Buskirk et al. 2014, Sniegula et al. 2019a), every other day we replaced ¼ of the water in the experimental containers holding damselfly eggs and larvae with water from an aquarium (55 × 35 × 45 cm) holding 3 perch (age 1 + y). In the control group, we replaced the same amount of water with aged tap water (Fig. 1). We captured perch from Dobczyce Lake (49°52′27″N, 20°2′55″E) several weeks before the experiment started and housed them with permission from the Local Ethical Committee (ref. 152/2018). We fed perch once/d with frozen Chironomidae larvae.

**Response variables**

We measured the following life-history variables: larval survival, development time, mass up to and at emergence, growth rate to final instar, and mass of the final instar as a function of emergence success. Larval survival was measured as the number of larvae alive after 2 wk and when entering the final instar. Survival until emergence was measured as the number of larvae that emerged successfully. Development time was measured as the number of days between hatching and emergence, and mass at emergence was measured as wet mass. The mass of the final larval instar and adult at emergence was measured as the wet mass of the larvae entering the final instar and as the wet mass of adult the day after emergence. Prior to weighing, we dried the larvae by blotting them with tissue paper. The growth rate to the final larval instar was measured as the mass of larvae entering the final instar/number of days between hatching and entrance into the final instar. We chose to measure mass and growth rate during the final instar because these values provided an additional mechanistic explanation for the life-history traits we measured at emergence. We used mass at emergence rather than adult structural size (measured, for example, as head width) as our measure of adult size. We note, however, that these 2 variables are used as surrogates for predicting insect fitness (Sokolovska et al. 2000, Stillwell et al. 2010). In addition, damselfly head widths of the final instar are correlated with adult head widths, and head widths are correlated with overall structural body size (Harvey and Corbet 1985, Corbet 1999). We used AS.62. R2 Plus Analytical Balance (Radwag® North Miami Beach, Florida) for larval and adult weighing.

**Statistical methods**

To measure the survival rate, we used a generalized mixed model with a binomial distribution using the glmer function in the lme4 package in R (version 6.3.1, R Project for Statistical Computing, Vienna, Austria; Bates et al. 2015). We used Wald χ² statistics to test for the fixed effects of 2 categorical explanatory variables: the presence/absence of fish cues in the egg and larval stages, and their interaction (Fox and Weisberg 2019). In case of substantial interaction terms, we assessed the differences between treatment levels using the emmeans function from the emmeans package in R (Lenth et al. 2020). To test for those same fixed effects of presence/absence of fish cues on development time (days), wet mass, and growth rate, we used linear mixed models implemented in the lme4 package with the lmer function (Bates et al. 2015). To measure whether there was a minimal mass the larvae had to reach to emerge successfully, we used a logistic mixed-effects model with a binomial distribution (glmer function) to test emergence success as a function of final-instar wet mass. We used family as a random effect in all models.

**RESULTS**

**Survival**

*2 wk* Survival of larvae for the first 2 wk after hatching was negatively affected by fish cues presented in the egg stage, but only when fish cues were also present in the larval stage (Fig. 2A, Tables 1, S1). Survival was reduced by 43% when only the larval stage was exposed to fish cues but was reduced by 75% when both the egg and larval stages were exposed to fish cues (Fig. 2A, Table S1). This result suggests an interaction between egg and larval fish-cue treatments, but the interaction had a negligible effect in our model (Table 1).

**Final instar before emergence** Survival to the final instar was 50% lower in treatments where fish cues were present during the larval stage. There was no substantial effect of fish cues received in the egg stage (Fig. 2B, Table 1). Hence,
as larvae developed and grew, the effect of fish cues received in the egg stage diminished.

**Emergence**  Survival to emergence was marginally affected by fish cues received in the larval stage (Table 1): larvae receiving fish cues showed lower survival than those that did not (Fig. 2C).

**Development time and mass at emergence**

There was a substantial overall effect of fish cues received in the larval stage on development time until emergence (Fig. 3A, Table 1). Larvae that received fish cues only in the larval stage took on average 6 d longer to develop than those that did not, and there was a similar difference in development time when fish cues were presented in both the egg and larval stages (Fig. 3A). In contrast, development time was not affected by fish cues received in the egg stage only, and there was no egg by larval fish cue interaction effect (Table 1).

There was no substantial effect of the treatments on wet mass at emergence (Fig. 3B, Table 1), suggesting that fish cues received during either or both egg and larval stages do not affect mass at emergence.

**Growth rate**

Growth rate based on mass when larvae entered the final instar was much lower in treatments where fish cues were present in either the egg or larval stage or both (Fig. 4, Table 1). For larvae that received no fish cues in the larval stage, growth rate was reduced by 13% when fish cues were presented in the egg stage. However, growth rate was reduced by a further 8% when fish cues were present in both the egg and larval stages (Fig. 4, Table S2). Hence, the effect of fish cues was stronger when they were received in both the egg and larval stages than when they were received in the egg stage only (Fig. 4). This finding suggests an interaction between egg and larval fish-cue treatments, but our analyses indicated the interaction was only marginal (Table 1).

**Emergence success by mass of final instar**

Wet mass at the final instar had a positive effect on larval emergence success (df = 1, $\chi^2 = 6.63, p = 0.01$; Fig. 5).

**DISCUSSION**

In this study we examined how the non-consumptive presence of a predator during the egg stage, larval stage, or both affect the life-history traits of the damselfly *I. elegans*. We found that indirect non-consumptive effects of fish cues decreased survival to emergence and the development time to emergence in the damselfly. These results correspond with those from previous studies (Tseng 2003, Hellmann et al. 2011, McCauley et al. 2011, Meadows et al. 2017) and, thus, further confirm that indirect non-consumptive effects are present in many animals with complex life cycles (Benard 2004). The novelty of our experiment was that we looked across 3 developmental stages: eggs, larvae, and adults. However, effects of the fish-cue treatments during the egg stage were not strong for any response variable measured in the
larval and adult stages, except larval growth rate to the final instar.

Survival until emergence was substantially affected by the presence of fish cues in the larval stage. Such an effect on survival until metamorphosis has also been found in other studies. For example, Baranowski and Preisser (2018) found that the non-consumptive exposure of luna moth larvae to predatory wasps resulted in increased luna moth mortality, McCauley et al. (2011) showed a strong non-consumptive lethal effect of fishes or predatory insects on dragonfly larvae, and Ower and Juliano (2019) showed that presence of chemical cues of the predacious elephant mosquito decreased eastern tree hole mosquito survivorship until emergence. Short-term behavioral and life-history studies often show that organisms are affected by fish cues (Silberbush et al. 2019, Sniegula et al. 2019a), but other studies have shown that the effects on behavior and growth decline over the long term (Dalesman et al. 2015). Here, we showed that the effects of fish cues experienced during either or both egg and larval stages persisted until emergence because survival up to emergence was reduced, suggesting that the non-consumptive effects come with high costs in terms of mortality.

Development time was substantially longer for damselflies receiving fish cues in the larval stage than those that did not. This longer development time was likely responsible for the lack of an effect of fish cues on mass at emergence. Hence, larvae that experienced stressful fish cues compensated for their slower growth by developing for a longer period of time. Similar results have been found in other damselflies (Johansson et al. 2001, Mikolajewski et al. 2005) as well as in other animals (Ball and Baker 1996, Wildy et al. 1999). Interestingly, Stoks et al. (2012) observed the opposite response in larval damselfly growth rate in the presence of invertebrate predator cues. These contrasting results could be caused by the functional difference in predators used in the studies. The slow development and growth we observed might be adaptive because the predator we used is not gape-limited (McCoy et al. 2011). In contrast, in the Stoks et al. (2012) study, the invertebrate predator used, a dragonfly larva, was gape-limited. Because damselfly larvae cannot reach a size refuge from predation by perch,
they probably reduce their foraging activity to reduce predation risk during the larval stage. A lower activity results in a lower encounter rate with food, but also a lower encounter rate with predators (Leonardsson and Johansson 1997). The former reduces growth and development and the latter reduces mortality risk. Reduced foraging activity in the presence of non-gape-limited predator cues is often found in insect larvae (Johansson et al. 2001, Davenport et al. 2014). In contrast, if the predator is gape-limited, potential prey might be able to grow to a sufficient size to reach a safe size refuge from predation (Urban 2008). In the absence of large top predators, such as fishes, individuals investing in rapid growth to reach a large size within a short time might have an advantage in terms of survival (Urban 2008). Nevertheless, larval development time is important for the adult stage because studies have shown that mating success is affected by the adult life span (Cordero et al. 1997, Thompson et al. 2011, Tuzun and Stoks 2018), and those individuals that emerge earlier during the favorable season are expected to have a longer life span (Rowe and Ludwig 1991).

We found that growth rate to the final instar was negatively affected by predation cues in the egg stage, although there were no other strong effects of fish cues being present only in the egg stage. In a previous study, we found that the stress imposed by the presence of fish cues during the egg stage increased egg mortality by ~60% in I. elegans (Sniegula et al. 2019a), suggesting that predation-risk stress in the egg stage can be high. Nevertheless, for those eggs that survived, we found that the larvae were able to compensate for this egg-stress effect, since they showed no differences in development time compared to the control larvae. Such compensation in life-history traits also occurs in other invertebrates (Dalesman et al. 2015, Fontana-Bria et al. 2017). Nonetheless, individuals exposed to fish cues during the short-lasting egg stage did not compensate for it in terms of increased larval growth rate. Rather, fish cues received during the egg and larval stages likely caused physiological stress or behavioral modifications that reduced growth (Johansson et al. 2001), and slower growth resulted in low emergence success and, thus, higher mortality at emergence. In fact, those individuals that emerged had a higher mass at final instar before emergence compared to those that did not emerge, indicating the existence of a threshold mass the larvae must reach to successfully emerge. However, compensation may come with costs. For example, individuals exposed to predation cues during the egg stage developed smaller wings than individuals not experiencing these cues (Fontana-Bria et al. 2017). Wing size commonly affects flight performance in insects, including damselflies (DeVries et al. 2010, Sacchi and Hardersen 2013). Interestingly, exposure to predation risk in the egg stage in the Ringed Salamander, Ambystoma annulatum Cope, 1886 resulted in reduced activity in larvae (Mathis et al. 2008),

Fig. 3. Development time of larval Ischnura elegans until emergence (A) and wet mass at emergence (B). Error bars represent ±1 standard error.

Fig. 4. Growth rate of larval Ischnura elegans to the final larval instar based on wet mass. Error bars represent ±1 standard error. 
suggesting that life-history traits are not the only traits affected by exposure to predation risk in the egg stage.

In summary, we show that non-consumptive predation stress during the egg or larval stage can have negative effects on key life-history traits through ontogeny. Thus, we showed carry-over effects of predator cues across the developmental stages of prey, indicating the importance of considering predation effects starting from the initial egg stage. Future experiments should focus on predation stress imposed separately and in concert at different life stages, as exposure to predator cues during different life stages may have different effects on the life history of prey species throughout development during their complex life cycles. Such effects may be important under natural conditions since predation risk often varies over space and time during an organism’s ontogeny (Tolon et al. 2009).

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