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Compensating for a bad start: compensatory growth across life stages in an organism with a complex life cycle

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Abstract: Organisms with a complex life cycle are characterized by a life history shift through metamorphosis, and include organisms such as insects and amphibians. They must optimize their use of resources and behaviour across different life stages in order to maximize their fitness. An interesting question with regard to such life history shifts is whether growth in the juvenile stage can be compensated for in the adult stage. Here we ask whether damselflies are able to compensate for depressed growth during the juvenile aquatic stage in their terrestrial adult stage. Damselflies emerge at a fixed adult body size, but feed during the adult stage and are thus able to gain mass as adults. We performed a mark recapture study in order to answer whether individuals that emerge from metamorphosis with a low mass are able to compensate by subsequent mass gain during the adult stage. Results showed that compensatory mass gain occurred in the adult stage such that small individuals gained more mass than large individuals. We also found that females gained more mass than males. However, individuals that emerged at a low mass still had lower mass as mature adults than individuals that emerged at a high mass, suggesting that compensation was not complete. This suggests that larval ecology and adult fitness are tightly linked and future research should focus more on elucidating the nature of this relationship.

Key-words: compensatory growth, complex life-cycle, habitat-shift, fitness, optimal body size and mass, damselfly, *Lestes sponsa*

Introduction

Many organisms have a complex life cycle that involves an abrupt change in an individual's morphology, physiology, and behaviour (Semlitsch et al. 1988; Rowe and Ludwig 1991). Examples of such organisms are amphibians and many aquatic insects that typically spend their larval stage in an aquatic habitat and their adult stage in a terrestrial habitat. These organisms experience trade-offs as they attempt to optimize their development to maximize fitness in each habitat. When environmental conditions in the larval stage are poor, larvae typically emerge to the adult stage at a smaller size and lower mass, and these life history traits are important for fitness (Rowe and Ludwig 1991; Honek 1993). For example, a higher mass is usually associated with higher fecundity in females. Therefore, an interesting question is whether individuals that experience poor growth conditions in the larval stage are able to compensate for this initial low growth in the subsequent adult stage. There are two main factors that might limit the ability for organisms to compensate in growth. First, the adult stage during emergence might be very time constrained in organisms such as insects that live in temperate areas because they have to mature and mate before the season ends (Rowe and Ludwig 1991). Second, compensatory growth usually incurs costs, such as higher oxidative stress (Metcalf and Monaghan 2001; De Block and Stoks 2008). Despite many theoretical (Yearsley et al. 2004; Mangel and Munch 2005) and empirical studies (e.g. Forsen et al. 2004; Dmitriew and Rowe 2005; Johnsson and Bohlin 2006; De Block and Stoks 2008; Auer et al. 2010), few studies have been performed on compensatory growth across life stages and under natural field conditions.

Males and females in many species differ in size and in many invertebrates females are larger than males (Anholt et al. 1991; Teder 2014). When female fecundity is size-dependent, the larger size of females is often interpreted in terms of fecundity selection (Blanckenhorn 2005). However, in some invertebrates males are larger than females. In the majority of these species males show strong intraspecific competition (e.g. male-male territorial competition), hence the larger size of males is interpreted as a result of sexual selection (Blanckenhorn 2005). Because males and females differ in size, they might have a different trade-off with

regard to growth in different life stages for organisms with complex life cycles (Crawley and Johansson 2002). For example, in species with a female biased size dimorphism, we could argue that relative mass increase should be higher in females than in males during the adult stage. Females should be able to allocate more time to foraging in order to gain weight while males should spend relatively more time searching for mates since that would increase their fitness relatively more than investing in mass increase.

In the present work, we study mass gain of newly emerged individuals of the damselfly *Lestes sponsa* (Hansemann, 1823). Damselflies have an aquatic larval stage that lasts for several months or years, and in *L. sponsa* the larval stage lasts for a couple of months (Askew 2004). The majority of growth and development occurs in the larval stage (Corbet 1980). Then they emerge as adults into the terrestrial habitat and reach sexual maturity after days or weeks. At emergence their exoskeleton is fixed and hence they cannot increase in size as adults. However, they might gain mass, since they feed as adults. Adult mass and size are important fitness components in damselflies (Sokolovska et al. 2000; Thompson and Fincke, 2002). In males it has been shown that increasing fat reserves increases mating success (Marden and Waage 1990) and Stoks (2000) showed that lifetime mating success was highest for males of intermediate size. In female damselflies, De Block and Stoks (2005) found that lifetime mating success increased with mass at emergence, and Richardson and Baker (1997) showed that females that consumed more food as adults produced more eggs. However, other life history traits are also important for fitness, e.g. Banks and Thompson (1987) found that 70% of the variation in life time reproductive success of females was explained by longevity in the adult stage. *L. sponsa* has a scramble mating system, where males are non-territorial, but compete in order to try to locate and mate with as many females as possible (Choe and Crespi 1997). In contrast, females try to avoid male harassment and spend most of their time foraging (Choe and Crespi 1997).

There have been very few field studies of mass gain after emergence under field conditions in adult damselflies or insects in general. Such information is important for a full understanding of life history ecology and fitness, not only in damselflies but also for any organisms with complex life cycles. Anholt (1991) found that females gained weight after emergence but that this increase was independent of mass at emergence, whereas mass change after emergence in males was a function of mass at emergence. Surprisingly small males gained weight while large males lost weight. In butterflies it has been shown that female butterflies compensate for poor larval nutrition by selectively feeding on food sources with higher amino acids, but no

such pattern was found for males (Mevi-Schutz and Erhard 2003). Karlsson (1994) showed that two nectar feeding butterflies showed a decrease in mass after emergence while a nectar and pollen feeding species showed an increase in mass after emergence. Hence, compensatory growths do occur in many insects, but it differs between sexes and species. In a review on Odonata, Anholt et al. (1991) found that all species increase mass after emergence, however that study did not focus on whether smaller individuals gained more mass than larger ones, hence no focus on compensatory mass gain.

The aim of this study was to examine whether individuals that emerge at a low mass/small size gain more mass in the adult stage than those that emerge at a high mass/large size. We predicted that those which emerge at a low mass/small size would gain more mass than those that emerge at a high mass/large size because those of the former category would try to compensate via more mass gain. We tested this by means of a capture-mark-recapture study in the field. A second aim was to answer whether males and females differ in their mass gain. Since males have to engage in competition for mating success and therefore have to spend more time searching for mates compared to females, we predicted that they will gain less mass relative to females during the adult stage.

Material and Methods

L. sponsa is a common damselfly distributed throughout Europe where it inhabits standing bodies of water such as open ponds with marginal emergent vegetation (Askew 2004). To estimate mass gain we performed a capture-mark-recapture study at a small pond (diameter 20 m) near Svartbäcken in Uppsala (59°52'54.43"N, 17°37'24.36"E), Sweden. *L. sponsa* is known to be a site-faithful species (Stoks 2000) and together with the fact that the study pond was in a geographically bowl shaped area, we assumed a low dispersal. The fieldwork for this study was conducted from July 6th to August 2nd 2014. This period corresponds to the emerging season of this species at this pond, since very few newly emerged individuals were seen before and after this period.

Capture-mark-recapture

Newly emerged adults were captured with a hand net on all days except rainy ones, put in a small plastic container with 3-4 pieces of vegetation, and then brought to the laboratory in a cool box. Newly emerged adults are easily recognized through their shiny wings and soft

bodies. Hence, the individuals captured emerged the same day we captured them and had not started feeding yet as adults. They were kept overnight in the laboratory under natural light conditions at a temperature of 18°C. The next morning, their size and mass was measured and every adult was marked individually. To measure their size, photos were taken on a grid paper, and body size estimates were taken later on from those photos using the program ImageJ (Rasband W.S., <http://resbweb.nih.gov/ij/>; NIH, USA), Fig. 1. To get an overall size, we measured the length of the thorax, wing, and abdomen as shown in Fig. 1.

Adult body mass was measured with a scale to the nearest 0.01 mg. All individuals were marked by coloured dots on their wings using permanent markers (Identi-Pen, Japan), allowing a unique marking pattern for each individual (Fig. 1). Handling and marking of damselflies has been shown to result in low mortality (Cordero, 1994a). Marked individuals were released back to the study pond on the day they were marked, and we waited a minimum of three days before we recaptured any marked individuals. This was to allow the damselflies sufficient time to gain mass. At the latitude of the study it takes *L. sponsa* about a week to reach sexual maturity at which time mating starts (unpublished results FJ). Münchberg (1933) reported a period of 10 days for this to occur in Polish *L. sponsa* populations. The maximum life span at the latitude is about 4 weeks (unpublished results FJ). If marked individuals were seen $\geq$ three days after they were marked and released, we recaptured them and brought them back to the laboratory to measure the change in their mass. Size was not measured again, since the size of damselflies is fixed after metamorphosis. It was not possible to mark newly emerging individuals on the first day of capture due to the risk of damaging their wings.

Statistical analysis

To get an overall body size estimate from the three size variables measured, we ran a Principal Component Analysis (PCA) using the correlation matrix on these variables and extracted the first PC as an overall measurement of body size. Mass gain of adults was estimated as absolute and relative mass gain. A *t*-test was used to compare the means of the body size and mass of newly emerged males and females. Linear regression models were used to look at the relationship between the initial size and initial mass respectively and the absolute and relative mass increase of recaptured individuals. Relative mass increase as calculated as percent. Initially we ran these models as multiple regression models with the time between capture and re-capture as an independent variable to control for the time difference of each recaptured individual. However, the number of days between capture and recapture had no significant effect in any of these models ($P > 0.22$, in all models), and

therefore we present our results without this variable. The PCA was run in Minitab 17 (2010) and all regression models and t -tests in RStudio (R Studio, 2012).

Results

In total, 344 (159 females and 185 males) newly emerged adults were captured and marked, of which 36 (10 females and 26 males) individuals were recaptured. The Principal Component Analysis (PCA) that was run on the body size variables of the 344 newly emerged individuals showed that PC1 explained 74 % of the variation and PC2 18 %. The loadings for PC1 and PC2 were 0.521, 0.59, 0.61, and -0.84, 0.48, 0.26 for thorax, wing and abdomen measurements respectively. We used PC1 for the overall size because it explained most of the variation.

Mass and size at emergence

There was a highly positive significant linear relationship between mass and size at emergence for both females ($r^2 = 0.43$, $n = 158$, $p < 0.001$) and males ($r^2 = 0.41$, $n = 185$, $p < 0.001$), Fig. 2. Mass at emergence was higher in females (33.35 ± 3.85 mg) than in males (29.21 ± 3.32 mg): $t = 10.597$, $df = 314.369$, $p < 0.001$. The female data set had one outlier (21 mg), and when this outlier was included in the analysis it did not change the results ($r^2 = 0.40$). There was no difference in size at emergence between the two sexes ($t < 0.001$, $df = 329.914$, $p = 1$).

Mass gain and size at emergence

Overall size (PC1 scores) at emergence and absolute mass gain were not significantly correlated in the 36 recaptured individuals ($r^2 = 0.00011$, $n = 36$, $p = 0.952$). Neither was overall size (PC scores) at emergence and relative mass gain correlated to each other in the 36 recaptured individuals ($r^2 = 0.047$, $n = 36$, $p = 0.20$).

There was a trend for a positive significant relationship between the overall initial size (PC scores) and mass at recapture in the 36 recaptured individuals ($r^2 = 0.11$, $n = 36$, $p = 0.051$). Mass at recapture was positively correlated with overall initial size (PC scores) in the 26

recaptured males ($r^2 = 0.32$, $n = 26$, $p = 0.002$; Fig 3a). In the 10 recaptured females, overall initial size (PC1 scores) and mass at recapture were not correlated to each other, but we note that we had a low sample size ($r^2 = 0.34$, $n = 10$, $p = 0.076$; Fig 3b). In summary our results suggest that initial size and mass gain are not correlated, and that individuals that have a large size at emergence have a larger mass later in life.

Mass gain and mass at emergence

No correlation was found between body mass at emergence and absolute mass change in the 36 recaptured individuals ($r^2 = 0.016$, $n = 36$, $p = 0.46$). However, there was a significant negative relationship when this was tested for males separately ($r^2 = 0.22$, $n = 26$, $p = 0.015$, Fig. 4a), but not for females ($r^2 = 0.05$, $n = 10$, $p = 0.49$; Fig 4b)). In contrast, relative mass gain was significantly correlated with mass at emergence in both males ($r^2 = 0.39$, $n = 26$, $p = 0.0005$) and females ($r^2 = 0.46$, $n = 10$, $p = 0.02$) (Fig. 5), suggesting that individuals which were lighter at emergence gained relatively more mass during the adult stage than individuals that emerged with a higher mass. However, when the analysis was run for all 36 recaptured individuals no correlation was found between body mass at emergence and relative mass increase ($r^2 = 0.047$, $n = 36$, $p = 0.2$). Females (52.64 ± 28.95 %) had a higher relative mass increase during their adult stage than males (28.27 ± 12.64 %) ($t = 2.57$, $df = 10.35$, $p = 0.02$).

In the 36 recaptured individuals, initial mass and mass at recapture were significantly correlated ($r^2 = 0.42$, $n = 36$, $p < 0.001$), Fig. 6. A positive correlation was found in males ($r^2 = 0.22$, $n = 26$, $p = 0.015$), but not in females ($r^2 = 0.05$, $n = 10$, $p = 0.49$), when the analysis was run for the two sexes separately. In summary, individuals with a low mass are able to compensate in mass, but they are not able to catch up in mass compared to those individuals that emerge at a larger mass since we found a positive relationship between individual mass at emergence and mass at recapture.

Discussion

Our results suggest that adults of *L. sponsa* are able to compensate for low mass at emergence from metamorphosis through both absolute and relative mass gain during the adult stage. However, although adults showed compensatory mass gain during their adult stage, the individuals that emerged at a lower mass still had a lower mass at maturation compared to those that emerged at a higher mass. Hence, although they compensate, they are not able to

fully catch up, which suggests that growth and development in the larval stage is an important adult fitness component. Our results suggests that the body size and mass of newly emerged adults depend on the food intake during the larval stage, and concur with results by De Block and Stoks (2005) in *Lestes viridis*, and Mikolajewski et al. (2015) in Coenagrionid damselflies. De Block and Stoks (2005) found that manipulation of time constraints and nutrient conditions in the larval stage affected time at emergence and body size which in turn affected life time mating success. Mikolajewski et al. (2015) found a negative relationship between growth and development rate in the larval stage and the length of the adult reproductive season across species, suggesting that species with longer adult stage can compensate more in terms of growth in the adult stage. Nevertheless, feeding and mass gain in the adult stage is important as shown in our study, since individuals emerging at lower mass gained more weight and Richardson and Baker (1997) showed that food intake in the adult stage was positively correlated with fecundity.

Compensatory growth, although beneficial, probably represents a non-trivial physiological cost for individuals (Stoks et al. 2006), which might explain why individuals were not able to show maximum compensatory mass gain. Though no studies have been looking at costs of compensatory growth in the adult stage, costs of compensatory growth have been shown in larval *Lestes viridis* (Stoks et al. 2006). They showed that larval damselflies were able to compensate for growth both under time (delayed photoperiod) and food (starvation) stress. However, individuals that compensated depleted their reserves of triglycerides and glycogen faster when exposed to starvation a second time, indicating a physiological cost. In future studies, costs of compensatory growth in each life stage should also be taken into account. Interesting potential costs in the adults stage would be higher predation risk and less time available for reproduction.

The body mass and size of newly emerged adults showed a strong positive correlation. Such a relationship is common in insects (Wickman and Karlsson 1989; Cordero 1994b) because a larger body can attain a larger mass which in turn affects fecundity and sperm conditions (Wickman and Karlsson 1989). Mass at recapture was positively correlated with both initial mass and initial size, showing that individuals that emerge at a smaller size and lighter mass have lighter body mass at recapture as well. However, both absolute and relative mass gain during the adult stage was only strongly correlated with initial mass and not with initial size, although initial mass and size were both strongly correlated to each other. This can be attributed to the fact that body size in the adult damselflies is fixed after metamorphosis, and

thus, does not influence mass gain during the adult stage as strongly as body mass at emergence does. In fact, the small exoskeleton of small individuals may not allow the same absolute mass increase as for large individuals because of exoskeleton limitations.

In accordance with our prediction, we found that females have a much higher mass gain rate during the adult stage than males do. This can be attributed to differences in mating behaviour between the sexes. *L. sponsa* is a scrambling species, in which males actively search for females (Choe and Crespi 1997). Thus, it can be predicted that it is advantageous for males to maximize their energy for growth during the larval stage in order to efficiently spend time to search for mates during the adult stage rather than to forage in order to continue growing (Andersson 1994; Stoks 2000). Females, on the other hand, spend more time further away from the pond in order to forage and avoid male-harassment, and only come to the periphery of the pond to mate and to deposit eggs (Choe and Crespi 1997). Hence, females will gain more mass during the adult stage relative to males, because they spend more time foraging and do not have to engage in mate searching as early in the season as males. This pattern of mass gain differences between males and females has been found in other damselflies as well (Anholt 1991; Anholt et al. 1991). A strong correlation between mass at emergence and absolute mass gain was only found in males and not in females, but the correlation between mass at emergence and relative mass gain was significant in both males and females. Future studies with a higher sample size are needed to establish whether the absence of a pattern between mass at emergence and absolute mass gain in females is real.

Our recapture probability was somewhat lower than that found in other studies on *Lestes* species. For example Stoks (2001) and Anholt (1997) reported recapture probabilities of between 0.1 and 0.5 in newly emerged adults. However, their estimates included capture during the first days after emergence which were not included in our recapture data. Differences in vegetation structure, population size and density could also influence differences in recapture rate between studies.

Understanding the link between larval ecology and adult fitness is crucial in animals with complex life cycles characterized with a habitat shift. Rowe and Ludwig (1991) showed in a theoretical model that a female emerging at a small size will end up having reduced fecundity, indicating the importance of growth during the larval stage to achieve high fitness later in life. So far, only few empirical studies have been able to demonstrate this relationship, partly because it is difficult to design an experimental setup that includes the larval and adult stage

of an organism. Richardson and Baker (1997) showed experimentally that final instar size in the damselfly *Ishnura verticalis* influenced developmental rates and adult size, but size did not influence fecundity. They therefore suggested that final instar larval size, which depends on the food consumption during the larval stage, is of relatively low importance for adult fitness components. However, it is premature to exclude the importance of larval ecology and size on later adult fitness, since the experimental setup of Richardson and Baker (1997) did not involve raising larvae with different food treatments, and thus it is uncertain what factors determined their size. Furthermore, several results support that larvae grown under high predation conditions reduce their movement and feeding and thus have retarded growth rate as well as low fecundity later in life (McPeck and Crowley 1987; Brodin and Johansson 2004, Peckarsky et al. 1993). In addition, the study by De Block and Stoks (2005) experimentally demonstrated a link between manipulated time and nutritional constraints during the larval stage and lifetime mating success during the adult stage in a damselfly. They showed that larvae grown under a natural photoperiod and high food level had higher lifetime mating success than larvae grown under delayed photoperiod and low food level, suggesting that growth and development in the larval stage is important.

Our results have demonstrated that although adult *L. sponsa* are able to compensate for mass gain, the adults that emerged at a low mass could not reach the mass of adults that emerged at a high mass, which suggests that the larval ecology of this species should not be ignored when fitness of adults are studied. Thorough investigation of how larval ecology influences adult fitness across insect genera remains a fertile area for future research.

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Figure Legends

Figure 1. Photo showing the size measurements taken on *L. sponsa*: 1) Thorax: Meso-episternum 2) Wing: Wingbase - pterostigma 3) Abdomen: 1st – 9th segment. The dots on the wings demonstrate the marking technique used to identify individuals upon recapture.

Fig. 2. The relationship between size at emergence and mass at emergence of newly emerged adults (○ and solid line females, and x and dashed line males).

Fig. 3. The relationship between initial size and mass at recapture in males (x and dashed line) and females (○). No line is given for females since $p = 0.076$ for the regression.

Fig. 4. The relationship between mass at emergence and absolute mass increase in recapture in males (x and dashed line) and females (○). No line is given for females since $p = 0.49$ for the regression.

Fig. 5. The relationship between mass at emergence and relative mass increase (○ and solid line females, and x and hatched line males).

Fig. 6. The relationship between mass at emergence (mg) and mass at recapture (mg) in recaptured individuals (○ and solid line females, and x and hatched line males).

FIG 1. Lee Hyeun-Ji and Frank Johansson

FIG 2. Lee Hyeun-Ji and Frank Johansson

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FIG 5. Lee Hyeun-Ji and Frank Johansson

FIG 6. Lee Hyeun-Ji and Frank Johansson