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Autotomy shapes the trade-off between seeking cover and foraging in larval damselflies

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Abstract Animals commonly choose between microhabitats that differ in foraging return and mortality hazard. I studied the influence of autotomy, the amputation of a body part, on the way larvae of the damselfly *Lestes sponsa* deal with the trade-off between foraging or seeking cover. Survival of *Lestes* larvae when confronted with the odonate predator *Aeshna cyanea* was higher in a complex than in a simple microhabitat, indicating that this more complex microhabitat was safer. Within the simple microhabitat, larvae without lamellae had a higher risk for mortality by predation than larvae with lamellae, showing a long-term cost of autotomy. When varying the foraging value (food present or absent) and predation risk (encaged predator or no predator) in the simple microhabitat, larvae with and without lamellae responded differentially to the imposed trade-off. All larvae spent more time in the simple microhabitat when food was present than when food was absent. Larvae without lamellae, however, only sporadically left the safe microhabitat, irrespective of the presence of the predator. In contrast, larvae with lamellae shifted more frequently towards the risky microhabitat than those without lamellae, and more often in the absence than in the presence of the predator. These decisions affected the foraging rates of the animals. I show for the first time that refuge use is higher after autotomy and that this is associated with the cost of reduced foraging success. The different microhabitat preferences for larvae with and without lamellae are consistent with their different vulnerabilities to predation and demonstrate the importance of intrinsic factors in establishing trade-offs.

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Introduction

Mobile foragers must often choose among microhabitats that differ in both predation risk and resource availability. Animals will often shift microhabitats or exhibit other behavioural changes in the presence of predators (e.g. Sih 1987, 1997). Relatively few studies, however, have examined whether this is associated with the cost of a lowered foraging rate (reviewed by Sih 1987; Lima and Dill 1990; Lima 1998). Gilliam (1982) suggested that foragers should choose sites with the lowest ratio of mortality rate to foraging rate, a proposal which was subsequently supported by experiments (Werner et al. 1983; Gilliam and Fraser 1987). The probability of survival is affected by intrinsic characters including age, size and sex (e.g. Werner et al. 1983; Abrahams and Dill 1989; Holtby and Healey 1990; Warkentin 1995; Gunnarsson 1998; Norrdahl and Korpimäki 1998). Therefore, the resolution to the trade-off between selecting safer or richer microhabitats can differ between conspecific foragers depending on their current condition (e.g. Werner et al. 1983; Abrahams and Dill 1989; Rochette and Himmelman 1996).

Autotomy, the amputation of a body part, is a widespread escape mechanism (see refs in Althoff and Thompson 1994). Despite the clear immediate survival value of autotomy as an escape mechanism (e.g. Formanowicz 1990), there are often long-term costs (e.g. Althoff and Thompson 1994 and refs therein). These costs may be reflected in habitat choice. Martin and Salvador (1992) showed that tailless lizards were more often associated with rocks than bare ground relative to tailed lizards and they hypothesized that this could be due to better escape probabilities there. They could, however, not detect an effect of this microhabitat shift on foraging rates (Martin and Salvador 1993; but see Martin and Lopez 1999).

Damselflies are characterized by the presence of three leaflike caudal lamellae that can be autotomized when grasped by a predator. The immediate contraction of a sphincter at a specialized breakage plane prevents the loss of body fluids and associated physiological costs (Legrand 1974). Larvae with lost lamellae have a reduced swimming ability, and hence a reduced escape-performance (Robinson et al. 1991a; Stoks 1999), and as a result are more vulnerable to predation (Robinson et al. 1991b; Stoks 1998a). In this paper I test how autotomy of larval lamellae affects the trade-off between seeking cover and foraging, by manipulating the lamellae of larval *Lestes sponsa* Hansemann in laboratory conditions. Members of this genus are characterized by their large lamellae (McNeill 1960). Within the genus, lamellae loss is high, up to 90% of individuals having at least one missing or regenerating lamella and almost 20% missing all three lamellae (Stoks 1998b). *L. sponsa* has a ‘fast’ lifestyle (sensu Johnson 1991). Lestidae can achieve rapid growth due to active searching for prey (Pickup and Thompson 1990; Krishnaraj and Pritchard 1995; R. Stoks, personal observation). Lestid damselfly larvae typically live in small temporary, or otherwise fishless, ponds (e.g. Gower and Kormondy 1963; Lutz 1968; Schneider and Frost 1996). In these ponds, aeshnid dragonfly larvae are partcularly important predators (e.g. Wellborn et al. 1996; Schneider 1997).

The specific hypotheses tested were as follows. (1) Because complex microhabitats will offer better refuges (e.g. Pierce 1988), I predicted that larval survival would be higher in complex than in simple microhabitats. (2) If larvae adjust their behaviour in the face of predation risk and foraging returns, I predicted that larvae would prefer the complex microhabitat more often in the presence of a predator and would leave it more often when food is added outside this microhabitat. (3) Because larvae without lamellae are more vulnerable to predation, I expected them to be more likely to avoid it, and would spend more time in the complex microhabitat and respond less to the presence of food than larvae with lamellae. (4) Finally, if food is only offered in the simple microhabitat, I predicted that differences between treatments in preferences for seeking cover would result in differential foraging rates. Hypothesis 1 was tested in experiment 1 with only one type of microhabitat offered, while hypotheses 2–4 were tested in experiment 2 by offering both a simple and a complex microhabitat while manipulating predation risk and foraging return in the simple microhabitat.

Methods

I collected final-instar larvae of *L. sponsa* in a pond near Antwerpen (northern Belgium) in May 1998. In the laboratory, larvae were held separately and starved for 24 h to equalize hunger levels. Only larvae without emergence signs (e.g. swollen wing paths and/or darkened eyes) and with three unregenerated lamellae were used in the experiments. I randomly assigned larvae to one of the two groups, autotomized lamellae and controls with lamellae. All three lamellae of experimental animals were removed by gently pulling them with two fingers until the animals autotomized these appendages. Control animals were handled similarly and underwent a sham operation. Penultimate-instar *Aeshna cyanea* starved and held separately for 24 h were used as predators.

Experiments were performed in boxes (15×10×11 cm), with aerated tap water (4 cm depth, 0.60 l) at 18°C. Boxes were wrapped with paper and lighted from above. This provided light in the boxes but prevented activity outside the boxes from affecting larval behaviour.

Experiment 1: effect of habitat complexity and lamellae autotomy on survival of larval *L. sponsa*

At the start of this experiment, one larva with and one without lamellae were placed together without food in the same box. Twenty boxes had a high habitat complexity (ten coiled polypropylene ropes 1 cm wide and 5 cm long), and twenty boxes had low complexity (three ropes). Twelve hours after the introduction of the damselfly larvae, one *A. cyanea* was introduced. Each replicate (*n*=40) ended when one of the larvae was killed by the predator or after 3 h. I recorded for the first attack of each dragonfly, the lamellae status of the victim and the capture efficiency (lethal or non-lethal). An attack is defined as a labium strike of the dragonfly larva towards one of the two damselfly larvae. Only first attacks were scored and analysed. After the experiment, the propensity of the *Aeshna* to eat was checked by offering them chironomid larvae.

Experiment 2: microhabitat choice and foraging success of larval *L. sponsa*

Individual larvae were subjected to a combination of three treatments: lamellae autotomy (present or absent), prey availability (no prey or 30 *Daphnia* added) and predation threat (no predator or a single *Aeshna* added). Each box was divided into three parts. One side had five coiled ropes (complex microhabitat), the opposite side had one rope on the bottom (simple microhabitat) and the middle compartment had a longitudinal rope linking both sides. The predator was placed within a translucent cup (diameter 5 cm, height 4.5 cm) in the centre of the simple microhabitat. This prevented the *Aeshna* preying upon the damselfly larvae and the *Daphnia* prey. The bottom of the cup consisted of a small netting (mesh size 250 µm). This enabled the larvae to see and smell the *Aeshna*; damselfly larvae respond to both visual and chemical stimuli from predators (Koperski 1997; Wisenden et al. 1997). To increase the spread of the chemical cues, each cup was lifted and gently lowered every hour. Identical cups, only containing water, were added in trials without predator, and also lifted hourly to overcome biases in movement patterns due to the presence and manipulation of cups. In all treatments, the simple microhabitat was more strongly illuminated to force the *Daphnia*, if present, to gather only in this side. Preliminary trials indeed showed that the abundance of *Daphnia* was highest in the low-complexity side (mean 26.8, SE 1.16, *n*=5), much lower in the middle part (mean 2.80, SE 1.02) and lowest in the high-complexity side (mean 0.40, SE 0.24). In two small experiments, I checked whether the strong illumination would affect the position of the larvae. First, in identical boxes without microhabitat, one side was strongly illuminated and the position of individual larvae was scored every hour for a total of 6 h (preference for the light side ranging from 0, complete light avoidance, to 6, complete light preference; a score not different from 3 indicates that the position of the larvae is neutral with respect to light). There was no effect of light intensity on the side selected by the larvae (mean preference for the light side 2.77, SE 0.21, *n*=30, one-sample *t*-test: *t*=1.10, *P*=0.28). Second, I repeated the experiment but added a complex microhabitat in one side of the box. In half of the boxes the complex side was strongly illuminated, in the other half, the other side was strongly illuminated. The strong illumination had no effect on the preference for the complex microhabitat (mean preference for complex side with strong light: 4.53, SE 0.24; without strong light: 4.67, SE 0.23; *t*=0.40, *n*=30, *P*=0.69). In all experiments, damselfly larvae were introduced gently in the middle part of the box; a predator was introduced 30 min later.

I ran 14 trials for each of the possible eight combinations of treatment levels. Each trial started at 1000 hours and ended after 8 h at 1800 hours. I monitored the microhabitat preference by recording each hour, the side of the box in which the animal was present. As a measure of preference for the high-complexity side, for each animal I used the sum of records within this side starting recording at 1200 hours. At the end of the experiments, I counted the number of surviving *Daphnia*.

Statistical analyses

I analysed the effect of microhabitat and lamellae status on the total number of attacks by the *Aeshna* with a log-linear analysis. Microhabitat preference (number of observations of each larva in the complex microhabitat) and foraging success (number of *Daphnia* eaten by individual larvae) were analysed using ANOVAs. Because the effects of lamellae status, food presence and predator presence are assumed to be multiplicative, I used the log link and Poisson error distribution in the GENMOD procedure of SAS 6.12 (SAS 1990). Overdispersion was automatically compensated for using the scale option. I tested whether larvae without lamellae make a different trade-off when choosing a microhabitat than larvae with lamellae by testing the three-way interaction between lamellae status, food presence and predator presence in an ANOVA with microhabitat preference as the dependent variable. To determine how each larva chooses between the microhabitats on the basis of the imposed trade-offs, I performed for each group separately an ANOVA testing for the main effects food presence and predator presence and their interaction. All means are given with their standard errors and all tests are two-sided with an α-level of 0.05.

Results

Experiment 1: effect of habitat complexity and lamellae autotomy on survival of larval *L. sponsa*

In the binary-choice experiment, a total of 39 *A. cynea* attacked one of the damselfly larvae. More larvae were attacked in the simple (39) than in the complex (0) microhabitat (log-linear analysis, $\chi^2=43.43$, $df=1$, $P<0.001$), consequently more larvae were killed by the *Aeshna* in the simple (18) than in the complex (0) microhabitat (binomial test, $P<0.001$). The number of attacks directed towards larvae with lamellae (19) and larvae without lamellae (20) was similar ($\chi^2=0.02$, $df=1$, $P=0.88$). However, the proportion of successful attacks on larvae without lamellae (70.0%) was more than three times that towards larvae with lamellae (21.1%) (log-linear analysis: $\chi^2=8.83$, $df=1$, $P=0.0030$).

Experiment 2: effect of lamellae autotomy, food and predator presence on microhabitat choice and foraging success of larval *L. sponsa*

On only 13 out of 784 possible occasions (7 observations×112 larvae) was a larva present in the middle compartment. Thus larvae not present in the simple compartment were in the complex one, and vice versa. The way in which the combinations of food availability and predator presence affected the microhabitat preference differed between larvae with and without lamellae (three-way interaction: food presence×predator presence×lamellae status, $F_{1,104}=12.35$, $P<0.001$; Fig. 1). Larvae without lamellae spent more time in the complex microhabitat when food was absent in the simple microhabitat (mean 6.61, SE 0.17) than when food was present (mean 5.50, SE 0.39; $F_{1,52}=7.05$, $P=0.011$; Fig. 1A). Predator presence did not affect the microhabitat preference of larvae without lamellae ($F_{1,52}=0.31$, $P=0.58$), nor was there an interaction between food presence and predator presence ($F_{1,52}=0.0048$, $P=0.94$). Larvae with lamellae also spent more time in the complex microhabitat when food was absent than when it was present (mean 6.25, SE 0.29 vs mean 3.11, SE 0.52 observations in complex microhabitat) ($F_{1,52}=8.60$, $P=0.0050$; Fig. 1B). In contrast with lamellaeless larvae, they also showed this behaviour in the presence compared to the absence of a predator (mean 5.43, SE 0.37 vs mean 3.93, SE 0.60; $F_{1,52}=5.94$, $P=0.018$). Moreover, the relative shift to the simple microhabitat when food was added was larger in the absence (77.8%) than in the presence (21.1%) of a predator (food presence×predator presence, $F_{1,52}=27.15$, $P<0.001$; Fig. 1B).

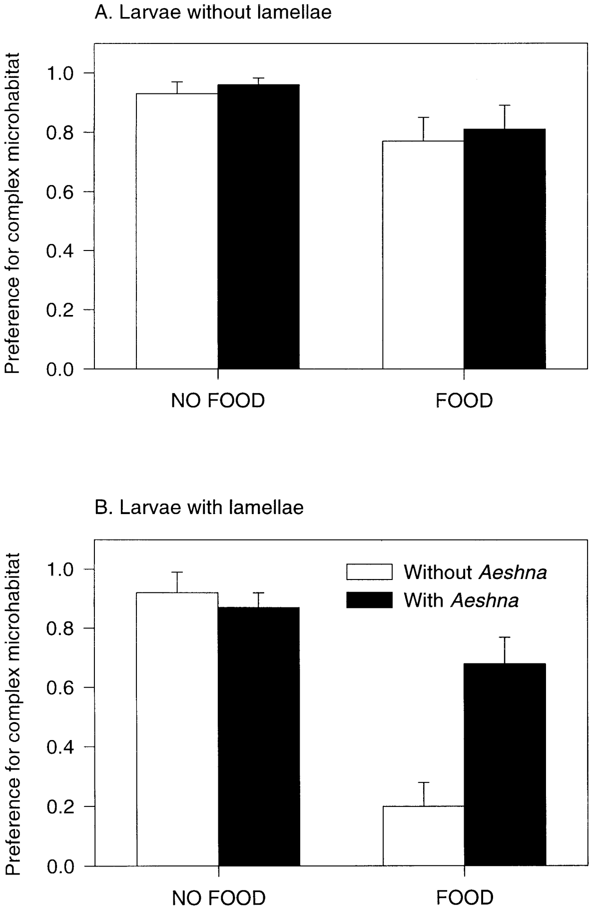

Fig. 1 Preference for the complex microhabitat in *Lesta sponsa* larvae (mean+1SE) in relation to food presence, non-lethal presence of *Aeshna*, and lamellae autotomy. **A** Without lamellae. **B** With lamellae

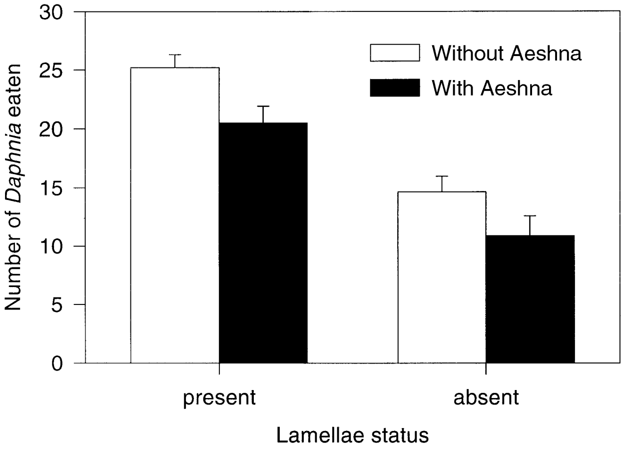

Fig. 2 Foraging success (mean+1SE) of *L. sponsa* larvae in relation to autotomy, and the non-lethal presence of *Aeshna*

In the presence of food, larvae that spent more time in the complex microhabitat had a lower foraging success (r=–0.60, n=56, P<0.001). Larvae without lamellae had a lower foraging success (mean 12.75, SE 1.12 *Daphnia* eaten) than larvae with lamellae (mean 22.86, SE 0.99; $F_{1,52}$=53.80, P<0.001; Fig. 2). To test whether this was due to a higher preference for the complex microhabitat and/or a reduced activity while in the simple microhabitat, the data were reanalysied with microhabitat preference as a covariate. Both the microhabitat choice (covariate: $F_{1,51}$=6.97, P=0.011) and the effect of lamellae status corrected for microhabitat choice ($F_{1,51}$=19.05, P<0.001) contributed to the lowered foraging success after lamellae autotomy. Foraging success was lower in the presence (mean 15.68, SE 1.43) than in the absence of a predator (mean 19.93, SE 1.32; $F_{1,52}$=11.69, P=0.0012). The relative drop in foraging success after the introduction of a predator tended to be larger in larvae without lamellae (25.8%) than in larvae with lamellae (18.7%) (lamellae status×predator presence, $F_{1,52}$=3.02, P=0.088; Fig. 2).

Discussion

The larvae responded to the conflicting demands placed upon them. As expected, the complex microhabitat was safer than the simple microhabitat. More complex habitats provide a better environment to escape predation by increasing the availability of hiding places and/or reducing predator foraging manoeuvres (e.g. Crowder and Cooper 1982; Hixon and Menge 1991). The lower number of observed attacks in the high-complexity microhabitat is due to a combination of both mechanisms. No *Aeshna* in the complex microhabitat attacked damselflies. This was not because these animals were more hungry; all dragonflies were starved for the same time and readily ate the chironomids offered directly after the experiment. This indicates they were unable to locate the damselfly prey during the experiment. Several *Aeshna* did locate their prey, but were not sufficiently agile in the-three dimensional network to position their head towards the damselfly to strike at it before the damselfly moved away. The negative correlation between the amount of time spent in the safe, complex microhabitat and foraging success demonstrated that staying longer in the safe, complex microhabitat indeed decreased food intake.

Larvae without lamellae had higher mortality rates than those with lamellae, confirming experiments with *Notonecta* as predator (Stoks 1998a; see also McPeek et al. 1996; McPeek 1997). This was expected, because these damselflies escape by swimming. Lamellae loss seriously impairs swimming performance (Stoks 1999). Autotomy of a limb associated with locomotion nearly always results in reduced escape performance (e.g. Formanowicz et al. 1990; but see Daniels 1983) and a higher predation risk (e.g. Dial and Fitzpatrick 1984; Wilson 1992; but see Althoff and Thompson 1994).

Prey commonly possess a diversity of antipredator behaviours, some of which are flexible, occurring only in the presence of a predator, while others are fixed (Sih 1987). When no food was present, all larvae stayed almost continuously (mean 91.8, SE 2.4%) in the safe, complex microhabitat. Wellborn and Robinson (1987) also found that in the absence of food, odonate larvae preferred safer sites. Adding food to the hazardous side induced larvae to switch strategies of habitat use at the cost of higher predation susceptibility. In larvae with lamellae this shift was flexible, because they stayed in the dangerous, food side significantly more in the absence than in the presence of the predator. This illustrates that damselfly larvae are able to assess differences in foraging profitability and predation risk and to balance the trade-off. A flexible response to increased predation risk has been found in other odonates (e.g. Heads 1986; Pierce 1988). In contrast, larvae without lamellae responded to their higher perceived predation risk with a steady high preference for the safe microhabitat, irrespective of the true predation pressure. Larvae without lamellae also compensated for their higher vulnerability with a fixed reduction in their number of moves (Stoks 1998a). These fixed antipredator behaviours are consistent with the prediction of Sih (1987) that prey should show more fixed behaviour if the predation risk is higher. Pierce (1988) showed that across odonate species and instars, the vulnerability to fish predation was more determined by their microhabitat use than by the predator-induced microhabitat shift. Instead of an adaptive explanation, there is also the possibility that after autotomy, larvae face physiological problems linked with respiration. However, lamellae play only a minor role in oxygen uptake of *Lestes* larvae (Eriksen 1986) and aerated tap water was used in all experiments.

The experimental results strongly suggest that staying longer in a safe microhabitat necessarily leads to reduced foraging if food is not evenly distributed (see also Martin and Lopez 1999). Furthermore, after correction for refuge use, the foraging success of larvae without lamellae was still lower than that of larvae with lamellae. The result may be explained by a fixed activity reduction after autotomy (Stoks 1998a), so that larvae without lamellae have a lower foraging success per unit time spent in the simple microhabitat. It is a common assumption that habitats with high rates of energy gain are also riskier (e.g. Ludwig and Rowe 1990) which often seems to be the case in nature (e.g. Werner et al. 1983; but see Henrikson 1993). There are two reasons to assume that my results may be transposed to the field situation where refuge and foraging sites may differ in food value, although probably not to such extreme degrees as in the experimental situation. First, microhabitats highly used by odonates in nature are safer, but not necessarily used as feeding sites (Wellborn and Robinson 1987). Second, because aeshnids and *Lestes* larvae eat the same prey (e.g. Fischer 1966, 1967; Blois 1985; Johnson 1985), they probably have the same preferred foraging sites.

Sih (1987) predicted that prey that escaped predation by using ephemeral macrohabitats in which important predators are rarely found, so called ‘fugitive prey’, should be fast developers. Members of the genus *Lestes* are very fast developers (Pickup and Thompson 1990) and are thus adapted to live in temporary ponds (Jödicke 1997) where fish are absent. *Lestes* larvae are very vulnerable to fish predation (e.g. Macan 1977). Within temporary ponds, *Lestes* larvae are, however, still confronted with invertebrate predators, such as dragonfly larvae of the genus *Aeshna* and notonectids (Schneider 1997). Shifting to refuges within a habitat to avoid encounters with predators constrains a fast lifestyle. Even when resource availability is high, organisms may not be able to take advantage of these resources because of the conflicting need to avoid predators (Sih 1987). This was indeed the case in my experiments: spending more time in the safer microhabitat when food was present was costly because it resulted in reduced foraging success of the damselfly larvae. Reduced foraging rates result in slower growth rates (Pickup and Thompson 1990; Stoks et al. 1999). Habitat drying is an important cause of *Lestes* mortality (Fischer 1967; Jödicke 1997) and retarded growth will increase the chances that the pond will have dried before larvae can emerge (see also Fincke 1994).

The results suggest that conspecific damselfly larvae differing in lamellae status make different decisions to balance the trade-off between foraging needs and predator avoidance. Other studies dealing with trade-offs between predation risk and feeding needs have suggested that organisms can adaptively balance these conflicting demands (Sih 1980; Werner et al. 1983; Gilliam and Fraser 1987; Anholt and Werner 1995). The results further suggest that intermediate predators such as *Lestes* larvae may face severe difficulties with maintaining their necessary fast lifestyle within fishless temporary ponds that contain large invertebrate predators.

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