Evolutionary Ecology (2019) 33:257–272
https://doi.org/10.1007/s10682-019-09979-y

ORIGINAL PAPER

Functional plasticity in lamellar autotomy by larval damselflies in response to predatory larval dragonfly cues

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Received: 11 September 2018 / Accepted: 1 March 2019 / Published online: 5 March 2019

Abstract

Adaptive autotomy is the self-amputation of an appendage in response to external stimuli that benefits survival. Variation in the ease of appendage removal among populations suggests that autotomy performance is under selection, evolves, or is phenotypically plastic, although the latter has never been experimentally tested. We model an autotomy threshold that optimally balances how the benefits of surviving predator attack versus the costs of losing an appendage vary with predator presence. We test for functional plasticity in autotomy threshold in the caudal lamellae of *Enallagma* damselfly larvae by experimentally manipulating non-lethal cues from predatory dragonfly larvae. Predator cues lead to functional plastic responses in the form of smaller lamellar joints that required lower peak breaking force. This is the first experimental demonstration of functional plasticity in autotomy to cues from a grasping predator, a novel form of indirect predator effects on prey, realized through plasticity in morphological traits that govern the autotomy threshold. This supports the model of optimized autotomy performance and provides a novel explanation for variation in performance among populations under different predator conditions. Plastic autotomy responses that mitigate costs in the face of variation in mortality risks might be a form of inducible defense.

Keywords Autotomy · Self-amputation · *Enallagma* damselflies · Predator indirect effects · Inducible-defense · Phenotypic plasticity · Evolution

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Electronic supplementary material The online version of this article (https://doi.org/10.1007/s10682-019-09979-y) contains supplementary material, which is available to authorized users.

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Introduction

Autotomy, the self-amputation of an appendage at a breaking plane in response to external stimuli followed by appendage regrowth, has evolved for a wide range of body parts and taxa (Arnold 1988; Fleming et al. 2007; Bateman and Fleming 2009; Seifert et al. 2012), providing opportunities to identify the mechanisms that shape variation in autotomy. The benefits of autotomy are increased chances of prey survival during encounters with grasping predators through escape (Cooper and Frederick 2010) and predator distraction (Robinson et al. 1970), and reduced mortality from infected or wounded body parts (Maginnis 2006; Fleming et al. 2007). Autotomy can also be costly when it results in death or otherwise reduces fitness by impairing future mobility, foraging, reproductive success, and predator avoidance, or when energy is required to resist infection and regrow an appendage (Congdon et al. 1974; Dial and Fitzpatrick 1981; Bellairs and Bryant 1985; Arnold 1988; Smith 1990; Robinson et al. 1991a; Stoks 1998; Maginnis 2006; Fleming et al. 2007; Naya et al. 2007; Bateman and Fleming 2009). The microevolution of autotomy is likely governed by benefits relative to costs but this has not been formally modeled to date.

Selection likely favours autotomy when the benefits outweigh its costs, and so the advantages of autotomy should be large to justify sacrificing body parts with major function (Arnold 1984, 1988; Gyssels and Stoks 2005; Bateman and Fleming 2009). Interspecific variation in ease of autotomy strongly suggests that costs and benefits shape variation in tail autotomy among lizards (Bellairs and Bryant 1985; Arnold 1988; Cooper et al. 2004). However, the benefits of autotomy relative to its costs are difficult to quantify, nor is it known whether costs and benefits may vary in ways that favour functional plasticity in autotomy (Arnold 1988; Bateman and Fleming 2009) that could also generate variation among populations.

Costs and benefits figure strongly in the evolution of autotomy because they are expected to generate important fitness trade-offs. For example, autotomy is limited to appendages that do not directly incur a high risk of lethality when lost (Bellairs and Bryant 1985; Arnold 1988; Cooper and Vitt 1991). However, non-lethal costs might also influence fitness when a lost body part influences organismal performance in other ways. For example, a body part can play multiple functional roles at different stages of a prey-predator interaction (Cooper and Vitt 1991). A swimming appendage autotomized in the resistance stage might functionally contribute to prey survival in future predator encounters by its contribution to predator avoidance. Appendage loss also reduces performance during feeding, reproduction, and intraspecific competition (Maginnis 2006; Fleming et al. 2007; Naya et al. 2007; Bateman and Fleming 2009). Furthermore, accidental autotomy can occur outside of a prey-predator encounters, such as when arthropods lose appendages during moulting (Maginnis 2006). Substantial survival benefits of autotomy are also required for it to be favoured by selection, but these need not be universal (Arnold 1988). For example, these benefits will be limited when predation is rare, when autotomy does not greatly increase the chances of eluding a predator, or when other anti-predator traits such as speed, agility, crypsis, size, and defensive weaponry make autotomy unnecessary.

Diversity in autotomy performance is expected among populations when the fitness consequences of appendage loss depend on local conditions in a way that generates diversifying selection (Cooper et al. 2004). For example, high predation risk may generate selection that favours autotomy but low predation risk should disfavor autotomy (Fig. 1). We also know little about how fitness trade-offs might generate antagonistic selection on autotomy traits within an environment. Under variable predation risk, autotomy can allow

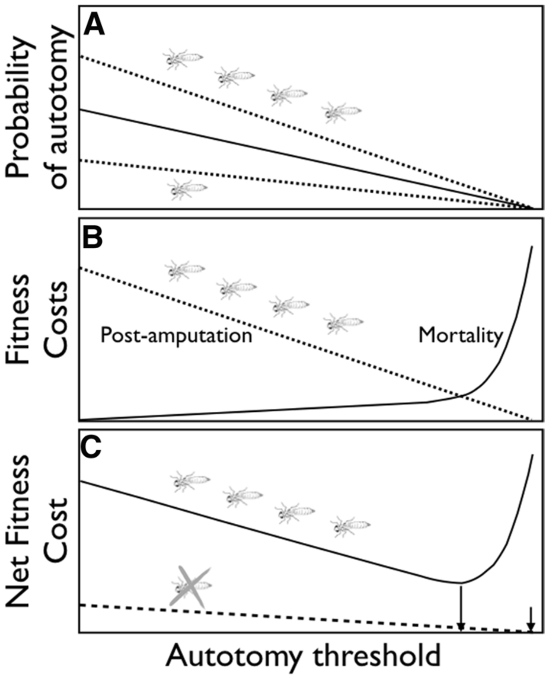

Fig. 1 An optimal autotomy threshold that balances the opposing forces of survival benefits of easy amputation against costs of amputation that also influence fitness. The autotomy threshold is a performance characteristic that links biomechanical traits that govern appendage loss to survival during the post-contact resistance phase of a prey-predator encounter. Traits that govern the threshold can be under antagonistic selection when the survival benefits of easy amputation are countered by any costs of amputation that influence fitness. An optimal autotomy threshold that balances these opposing forces should vary with changes in the local environment that influence the benefits relative to costs (complete model in the supplementary material 1). **a** The autotomy threshold governs the probability of autotomy, p(A), through internal biomechanical and neuro-muscular traits that set an upper threshold above which autotomy never occurs (solid line). However, p(A) is also influenced by external factors, such as local predation risk. Many versus few active grasping predators (shown as dragonfly larvae here) will increase or decrease p(A), respectively (dotted lines). **b** When grasping predators are present, the autotomy threshold governs a trade-off between the immediate probability of mortality, p(M), from a grasping predator that increases as the autotomy threshold increases (solid line), and the risk of incurring post-amputation costs, p(C), which occur in direct proportion to p(A). Thus, p(C) declines with higher autotomy thresholds (dotted line). **c** The optimal autotomy threshold minimizing the net fitness costs varies with conditions that influence the costs and benefits of autotomy. When grasping predators are rare, fitness is maximized by avoiding the costs of accidental autotomy, thus favouring a higher autotomy threshold (dashed line). When predation risk is high (solid line), fitness is maximized by a balance between avoiding mortality through autotomy and minimizing costs, thus favouring a lower autotomy threshold

an individual who encounters a predator to survive, but another individual who does not encounter a predator may produce more offspring by keeping its appendage (Robinson et al. 1970). The traits that govern autotomy performance might come under antagonistic selection because easier autotomy is beneficial in one but not the other situation and selection is governed by the genotypic fitness averaged across all conditions. Under these conditions, plasticity in autotomy might be favoured when it allows an individual to reliably match autotomy performance to local conditions and avoid unnecessary costs. As far as we know, adaptive plasticity in autotomy has not been formally considered.

Optimality approaches have provided valuable insights into the evolution of a variety of anti-predator traits (Lima and Dill 1990; Cooper and Vitt 1991; Cooper and Frederick 2010), and so we apply such an approach here to evaluate how autotomy performance might respond to changes in costs relative to benefits arising from variation in predation risk (supplementary material 1). We focus on the autotomy threshold, a performance characteristic that is influenced by morphological and neurological traits that resist appendage loss up to a threshold stimulus above which they permit the appendage to break away. A variety of such traits have been identified (e.g., Legrand 1974; McVean 1976; Wasson et al. 2002; Clause and Capaldi 2006; Fleming et al. 2007). These traits come under antagonistic selection when their functional effects on ease of autotomy contribute survival benefits but also generate significant indirect costs to fitness through effects of limb-loss on performance in other situations. Depending on local conditions, selection on traits that govern ease of autotomy may become stronger or weaker, shifting traits that govern the ease of autotomy (Fig. 1 graphically summarizes the results presented in the supplementary material 1).

We illustrate the shifting balance of the autotomy threshold using a larval damselfly system. Aquatic larvae have three leaf-like caudal lamellae connected to the posterior of the abdomen. These appendages autotomize at a breaking plane in the lamellar joint (Legrand 1974). The plane fails when sufficient force is generated by the pull between a grasping predator and a resisting prey. Peak lamellar joint breaking force is positively related to lamellar joint size and joint cuticle thickness after adjusting for body size (Burnside and Robinson 1995; Gleason et al. 2014). Similar characteristics govern limb autotomy in other invertebrates (Fleming et al. 2007). Features that weaken joints permit easier joint failure when the appendage is grasped and prey escape, but may also increase risk of accidental autotomy. Features that strengthen joints reduce the risk of such costs. Variation among larval damselfly populations in the autotomy threshold and in joint morphology are consistent with a shifting balance between opposing selection in different environments (Bose and Robinson 2013; Gleason et al. 2014), and also in lizards (Cooper et al. 2004).

The autotomy threshold can change either through evolutionary responses of populations or through plastic responses by individuals, although as far as we know, the latter has not been evaluated (Arnold 1988; Bateman and Fleming 2009). Variation in predation risk can favour the evolution of a variety of inducible anti-predator responses (Benard 2004; Johansson and Stoks 2005), whereas permanent changes in predation risk are more likely to promote the evolution of inflexible anti-predator traits (Benard 2004; Whitman and Agrawal 2009). Plastic responses in autotomy threshold could be generated by various physiological or developmental mechanisms that weaken the biomechanical properties of a breakage plane and so permit easier ‘passive’ rupture when an appendage is grasped (Bellairs and Bryant 1985). Alternatively, neuromuscular mechanisms can allow individuals to ‘actively’ control shedding of an appendage in response to cues (McVean 1976; Matthews et al. 1999; Wasson et al. 2002; Clause and Capaldi 2006).

We develop an optimality model that balances the costs and benefits of autotomy to qualitatively predict how the autotomy threshold changes with predation risk. We hypothesize that larvae can sense local predator cues and respond by adjusting the autotomy threshold. Our model predicts that larvae reared with grasping predators will have a lower autotomy threshold that is achieved either by smaller joints and weaker joint cuticles compared to control individuals reared without these predator cues. We then experimentally manipulated predatory dragonfly cues to test for functional plasticity in lamellar autotomy threshold and lamellar joint features in larval Coenagrionid damselflies (Odonata: Zygoptera).

Materials and methods

Larval damselfly functional ecology

Larval damselflies are ideal for tests of plasticity in autotomy. Larvae of various species detect and respond to predator cues by changing spine morphology (Arnqvist and Johansson 1998; Johansson 2002; Johansson and Stoks 2005) and behaviour (McPeek 1990a; Chivers et al. 1996; Koperski 1997; Wisenden et al. 1997; Mortenson and Richardson 2008; Brown and Robinson 2016). Plastic responses can also be matched to predator conditions because the aquatic larval period provides up to 10 developmental instar stages in which to detect and respond to local predator cues (Anholt and Werner 1995; Berrigan and Scheiner 2004; Whitman and Agrawal 2009).

Performance trade-offs are likely because caudal lamellae and their connecting joints serve multiple functions, such as generating thrust during swimming (Robinson et al. 1991b), enhancing gas-exchange (Eriksen 1986) and in signaling (Johnson 1991). Lamellar autotomy permits escape and survival during the post-contact resistance phase with attacking dragonfly larvae (Odonata: Anisoptera; Baker and Dixon 1986; Stoks 1998; McPeek 1990a). However, lamellar loss also reduces survival (Stoks et al. 1999) by limiting swimming performance (Robinson et al. 1991b; Burnside and Robinson 1995; McPeek et al. 1996; Stoks 1999a; Gyssels and Stoks 2005), impairing predator avoidance (Robinson et al. 1991a; McPeek 1997; Gyssels and Stoks 2005), increasing cannibalism (Stoks 1998), and reducing foraging (Stoks 1999b) and growth (Stoks 2001).

Furthermore, damselflies can experience uncertainty in predation risk between generations as a result of indiscriminate ovipositing in ponds with and without fishes. Larvae face two general classes of predators that impose diversifying selection on anti-predator traits: large predatory fish that consume their prey whole and large predatory invertebrates that grasp their prey, such as dragonfly larvae, and dominate invertebrate predation in fishless lakes (McPeek 1990a, b; McPeek et al. 1996; Strobbe et al. 2011). Easier lamellar autotomy enhances survival under predation from dragonflies but is ineffective against fish (Baker and Dixon 1986; McPeek 1990a). When a landscape contains accessible ponds dominated by one or the other predator, then indiscriminate ovipositing behaviour can expose larvae to unpredictable predator environments between generations. While many damselfly species appear to have high ovipositing site fidelity, this is not universal (e.g., McPeek 1989; Brown and Robinson 2016), in which case a lower autotomy threshold beneficial under dragonfly predation may be inappropriate in a fish predator environment.

Specimen identification, instar stage and collection

Our experimental larvae were from the *Enallagma ebrium* (Hagen)/*E. hageni* (Walsh) species-pair (hereafter ‘*Enallagma*’) used in prior studies of the biomechanics of lamellar autotomy (Gleason et al. 2014). Identification was based on the Odonata Larvae of Michigan key (Bright and O’Brien 1999). Larvae of these species cannot be reliably distinguished based on morphological or mtDNA features (Turgeon and McPeek 2002). As far as we know, genetic identification based on nuclear genes has not been attempted and was beyond the scope of this study. We treated the two *Enallagma* species as identical, assuming similar potential for plastic developmental responses, similar larval life histories, rates of development and trait allometries. Random application of treatment ensured that any species effects would not confound experimental treatment. Our inability to distinguish species may have two important drawbacks. If no experimental effect is observed, we will not be able to distinguish whether plastic responses are absent or whether species differences obscured the response. If plastic responses are observed, we cannot definitively assign this to one or both species.

Both species have adaptations beneficial to ponds with fishes, however, ovipositing by *Enallagma* can also be locally indiscriminate (McPeek 1989, 1990b; McGuffin et al. 2006). In our region, they are present in ponds with and without predatory fish (Brown and Robinson 2016). Larvae develop rapidly through the fall from eggs laid in mid-summer and overwinter at late instar stages −6 to −2 (Ingram and Jenner 1976), resuming growth in the spring to emerge in the early-mid summer (Kormondy and Gower 1965; Ingram and Jenner 1976). We estimate experimental larvae here to be in the −3 stage because mean starting head width was 1.84 mm (±0.221 s.d.), below the 3.35 mm size of final instars (see our methods and Fig. 1a in Ingram and Jenner 1976), and because no experimental larvae metamorphosed here despite some individuals undergoing three moults (mean moult number = 1.67, ±0.63 s.d.).

Experimental *Enallagma* damselfly larvae were sampled up to mid-October 2014 from ponds containing centrarchid sunfish near the city of Guelph in southwestern Ontario, Canada. We used larvae from ponds with fish where larvae were abundant because our goal was to test for a plastic response to the application of a dragonfly predator cue rather than plastic responses in its absence. Fish status in ponds was based on a minimum of four minnow fish traps deployed for at least 100 trap hours per pond (unpublished data, BW Robinson). Live damselfly larvae were collected by sweeping a D-net through shoreline aquatic vegetation in less than 1 m of water. Predatory *Aeshna* larval dragonflies were collected from a nearby fishless pond with minnow traps.

Experimental design

We tested for plasticity by systematically allocating *Enallagma* larvae to one of two predator cue treatments in the laboratory: (1) presence of a larval *Aeshna* dragonfly, segregated to prevent direct predator–prey interactions (predator treatment), or (2) absence of larval dragonfly (control). Individual damselfly larvae were housed in plastic containers (5.5 cm × 5.5 cm × 3.5 cm depth) with perching sticks. Three mesh-covered windows (3 cm × 3 cm on two sides and 4.5 cm × 4.5 cm on top) allowed the exchange of chemical and visual dragonfly cues, but prevented direct interactions. Sets of five damselfly containers were immersed within a larger tank (29 cm × 23 cm × 20 cm depth) filled with 5 L of 50% well water and 50% pond water from the natal pond (aerated and circulated with an air stone). A quarter of the tank volume was replaced with fresh well water each week. A 9 h light:15 h dark cycle was maintained with room lights, however, two additional 60 W incandescent bulbs were suspended 1 m above the tanks halfway through the experiment to increase water temperature (from 20 to 22 °C) in order to increase development rate. The experimental duration was 74 days (starting Oct. 28, 2014) in order to permit up to three moults during which plastic responses could be expressed (under ideal conditions, *Enallagma* have a 3-week instar duration; M.A. McPeek, personal communication).

The predator treatment included a single large free-roaming *Aeshna* dragonfly larva added to the larger external tank. The no-predator control treatment was identical to the predator treatment except for the absence of the predatory dragonfly larva, which was replaced by a sixth experimental damselfly larva to hold total resident odonate density constant between treatments. Each tank with a single predatory dragonfly larva was provided with three feeder *Enallagma* damselfly larvae on each of 5 days per week, which were consumed within 24 h. Each experimental damselfly larva was fed four large live *Daphnia magna* every second day. Treatments were randomly assigned to the whole tank and replicated eight times for a starting total of 88 experimental damselfly larvae (predator treatment = 40, control = 48).

Experimental damselfly larvae were replaced for either of two reasons. First, damselfly larvae that died were replaced to keep total larval density constant between treatments. Replacement larvae added in the first 5 weeks were treated as experimental larvae and included in analyses to increase sample size. Larvae replaced after 5 weeks were not analyzed because of their shortened exposure to treatment conditions. We recorded mortality, replaced dead larvae, and removed moulted exoskeletons during inspections every 2 days. Second, we replaced any experimental larvae that underwent two moults (with a placeholder larva) because this met our minimal developmental requirement (mean time to 2nd moult = 34.4 days, s.e.m. = 2.7; treatment $t_{27.9} = 1.45$, $P = 0.16$). Removed individuals were prepared for tensile testing (below) after an additional minimum 24 h sclerotization period to allow cuticles to harden (M.A. McPeek, personal communication). At the end of 74 days, all remaining experimental larvae were tested. Tensile testing was not performed on any experimental larva that died in its container.

Tensile testing

Our method focused on ‘passive’ rupture autotomy because we used freshly euthanized individuals for tensile testing. The lamellar joint breaking force in milliNewtons (mN) was measured on a single non-regenerated lateral lamella on each specimen using a benchtop Instron Model 3343 Universal Testing Machine (Illinois Tool Works, Glenview, USA). The preparation, mounting, and tensile testing of the lamellar joint closely followed methods described in Gleason et al. (2014; see their Fig. 5). While still moist, the mounted specimens were strained at a rate of 2 mm s^{-1} until autotomy occurred. Time, extension, and force data were recorded at 10 Hz. Bluehill software (Instron Corp. v2.9, Norwood, USA) was used to estimate the peak force in mN, which we interpret as the force required to break the joint. The head, thorax, abdomen, and any detached lamellae were subsequently preserved in 95% ethanol for measurement (below).

Imaging, body size, and joint morphometrics

Allometric relationships exist between larval head and body size, lamellar joint size, and lamellar joint breaking force (Bose and Robinson 2013; Gleason et al. 2014). Predator cues can also indirectly affect larval growth (Stoks 2001; McCauley et al. 2011) with potential effects on lamellar joint size and breaking force. Larval head width was used as a proxy for body size here (Ingram and Jenner 1976; Dixon and Baker 1988). Digital photographs of the head and the lamellar joint of detached lamella were made for each experimental larva against a scale through a dissection microscope. Maximum head width and maximum joint diameter were estimated from photographs using ImageJ software (v1.45 s, National Institutes of Health, Bethesda, USA). Growth (estimated as starting minus ending head widths) was compared between treatments to evaluate indirect predatory treatment effects. Lamellar joint cuticle area was estimated from the joint breakage surface of the detached lamella from a subsample of 17 individuals with cleanly broken joints from each treatment (see

Fig. 3 in Gleason et al. 2014) and imaged using a Hitachi S-570 Scanning Electron Microscope (SEM; Tokyo, Japan) at 10 kV. Total cuticle area exposed at the breakage plane was measured blind to treatment from SEM images of an autotomized lamella by subtracting the inner from the outer cuticle area following Gleason et al. (2014).

Statistical analyses

Rate of larval mortality was greater in the predator compared to control treatment (see results), and data on growth, morphology and lamellar joint breaking force were not always available for each larva due to some failed tensile tests. Sixty-three experimental larvae survived the experiment out of the original 88 (original = 47: predator = 15, control = 32; replacements = 16: predator = 9, control = 7). Of these, 46 larvae yielded valid breaking force measures (original = 37: predator = 14, control = 23; replacements = 9: predator = 4, control = 5). Preliminary analyses revealed no significant differences in growth or lamellar features among replicate tanks within treatments. Since small sample sizes and unbalanced design reduce statistical power, we combined individual damselfly larvae across replicate tanks, treating larvae as the replicated unit for analysis.

Peak breaking force was compared between treatments with ANCOVA using final head width as covariate, while joint cuticle area was compared accounting for covariation in joint diameter. Nonsignificant ($P > 0.05$) treatment × covariate interactions were removed. We also tested for treatment effects on the covariation between joint diameter and cuticle area with MANCOVA using head width as a covariate.

Indirect predator effects on larval growth, development, and survival are common in odonate larvae, and so we were also explored relationships between autotomy performance and other non-lethal effects of cues. Mortality rate was compared between treatments using a log-rank test of hazard differences. Two components of larval growth were compared between treatments: total growth and average growth per moult (individual total growth divided by number of moults). Differences in head width between treatments at the start and end of the study and differences in the total growth and mean growth per moult were each tested with ANOVA. Moulting frequency was compared between treatments using a two-sample Kolmogorov–Smirnov test, and mean time to first and second moult were compared between treatments with unequal variance t-tests. The effect of treatment on the relationship between average growth per moult and total number of moults was evaluated using ANCOVA, treating moult number as a covariate.

Analyses were performed with JMP Pro12. We accounted for variation between original and replacement subsets of experimental larvae in all analyses (excluding the analysis of mortality rate) by including a block factor. We report 2-tailed P-values in tests of mortality, growth, and moulting, but 1-tailed P-values for tests of breaking force and joint morphology because our functional biomechanical hypotheses make directional predictions.

Results

Lamellar joint performance and trait variation

Peak breaking force of lamellar joints was reduced in larvae from the predator compared to control treatment. The allometric relationship between peak breaking force and head width did not differ between treatments (ANCOVA treatment-head width

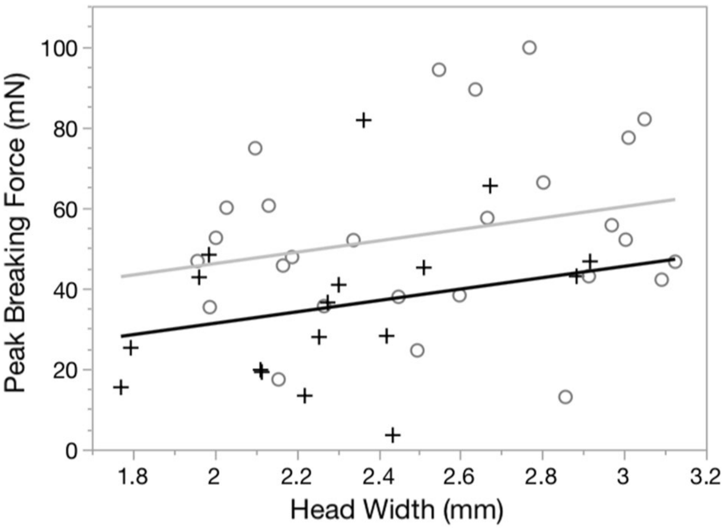

Fig. 2 Relationship between peak lamellar joint breaking force (mN) and head width (mm) of larvae in two treatments: predator (exposed to cues from larval dragonflies: crosses and black line) and control (no predator cue exposure: open circles and grey line). ANCOVA Treatment: $F_{1,54} = 3.12$, $P_{\text{1-sided}} = 0.04$; treatment × head width interaction: $F_{1,53} = 2.49$, $P = 0.12$

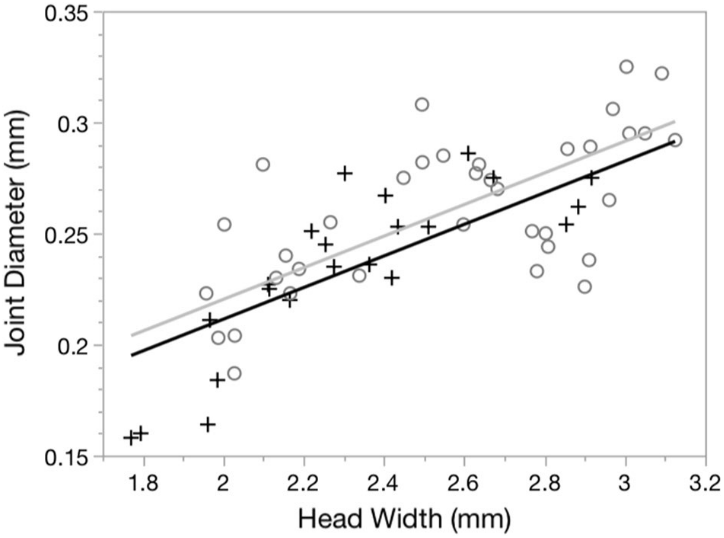

Fig. 3 Relationship between lamellar joint diameter (mm) and head width (mm) of larvae in two treatments: predator (exposed to cues from larval dragonflies: crosses and black line) or control (no predator cue exposure: open circles and grey line). ANCOVA treatment: $F_{1,42} = 4.72$, $P_{\text{1-sided}} = 0.02$; treatment × head width interaction: $F_{1,41} = 0.36$, $P = 0.55$

interaction: $F_{1,41} = 0.36$, $P = 0.55$). The joints of larvae reared with predator cues broke at an average force of 14.4 mN, 29% less peak force than required to break joints of larvae reared in the control treatment after accounting for variation in head width (treatment: $F_{1,42} = 4.72$, $P_{\text{1-sided}} = 0.018$; Fig. 2).

Lamellar joint diameter at the breakage plane was on average 5% lower in predator exposed larvae than control larvae after accounting for head width (treatment: $F_{1,54} = 3.12$, $P_{\text{1-sided}} = 0.04$; Fig. 3). The allometric relationship between joint diameter and final head width did not differ between treatments (treatment × head width interaction: $F_{1,53} = 2.49$, $P = 0.12$). Treatment also did not influence the relationships between joint cuticle area and joint diameter (treatment × joint diameter interaction: $F_{1,29} = 1.15$, $P = 0.29$), nor mean cuticle area after accounting for joint diameter (treatment: $F_{1,30} = 0.65$, $P_{\text{1-sided}} = 0.22$). Cuticle area and joint diameter were positively correlated after accounting for variation in head width (partial $r = 0.46$), but this was not influenced by treatment after accounting for variation in head size (MANCOVA $F_{2,29} = 0.083$, $P = 0.92$).

Survival, growth, and development

Damselfly larvae in the predator treatment died at almost twice the rate (25 out of 40) of those in the predator-free control (16 out of 48) (hazard log-rank $\chi^2 = 8.3$, $P = 0.004$). Of these, nine experimental larvae in the predator treatment and seven larvae in the control treatment were replaced within the first 5 weeks. The remaining 25 mortalities were replaced in the second 5-week interval and were not included in analyses.

Predator treatment also affected larval growth. Total larval growth assessed as change in head width was 27% greater in control compared to predator exposed larvae ($F_{1,55} = 4.25$, $P = 0.044$; adjusted mean and s.e.m., control = 0.736 ± 0.054 mm; predator = 0.579 ± 0.058 mm). An initial 8% greater head size in control larvae ($F_{1,55} = 4.44$, $P = 0.04$) did not contribute to the difference in growth because control larvae with starting head width ≤ 1.7 mm (i.e., no difference between treatments: $F_{1,21} = 1.50$, $P = 0.23$) still grew 31% more than those in the predator treatment ($F_{1,21} = 4.66$, $P = 0.043$; mean total growth control = 0.97 ± 0.097 mm; predator = 0.74 ± 0.078 mm). Growth differences did not result from a greater number of replacements by smaller larvae in the predator treatment because final head width was still 16% greater in the original control compared to predator larvae after excluding replacement larvae ($F_{1,40} = 9.30$, $P = 0.004$; mean control = 2.57 ± 0.069 mm; predator = 2.22 ± 0.092 mm).

Predator cues did not influence developmental rate despite faster growth by control larvae. Neither the frequency of moults ($KS_D = 0.147$, $P = 0.89$) nor the mean time to moult differed between treatments (time to first moult: $t_{79.4} = -0.57$; $P = 0.57$; or to second moult: $t_{27.9} = 1.45$; $P = 0.16$). Individuals who moulted more grew on average less per moult than those with fewer moults (linear regression of growth per moult against number of moults: $t_{56} = -4.95$, $P < 0.0001$), but this trade-off was not influenced by treatment (ANCOVA treatment: $F_{1,54} = 1.91$, $P = 0.17$).

Discussion

Our optimality model qualitatively predicted changes in autotomy threshold based on antagonistic selection operating on traits that govern autotomy. The model was supported by our empirical tests for functional plasticity in autotomy threshold in *Enallagma* damselfly larvae where we experimentally manipulated cues from predatory *Aeshna* dragonfly larvae. These results demonstrate that predatory dragonfly larvae can have novel non-consumptive effects on prey damselfly larvae that include plastic autotomy responses, in addition to reducing larval growth and survival as found elsewhere. They also suggest that intraspecific variation in lamellar joint size and breaking force observed among larval populations in the field may reflect functional plastic responses to local differences in predator communities.

A key prerequisite of adaptive plasticity is the capacity to detect and respond to local conditions to increase functional performance and fitness (Benard 2004; Whitman and Agrawal 2009). Functional plastic responses by individual *Enallagma* damselfly larvae here and elsewhere demonstrate that this prerequisite is frequently met (McPeek 1990a; Chivers et al. 1996; Koperski 1997; Wisenden et al. 1997; Mortenson and Richardson 2008; Brown and Robinson 2016). Many aquatic insects detect and respond to kairomones released by predated conspecifics (Chivers and Smith 1998; Johansson and

Stoks 2005) but visual cues are also possible and so we do not know what cues were involved here.

Plasticity in autotomy requires plasticity in the morphological features that govern the failure of the lamellar joint breaking plane. Experimental manipulation of dragonfly predatory cues induced shortened lamellar joint diameters and reduced peak breaking force compared to predator-free control larvae as we expected. To our knowledge, this is the first evidence of functional plasticity in an autotomy threshold directly induced by cues from a grasping predator. It also indirectly supports the functional link between lamellar joint morphology and autotomy threshold. Prior studies found that cuticle thickness also influences lamellar joint breaking force (Gleason et al. 2014), but we found no evidence that cuticle thickness responded to predator cues after controlling for joint diameter here, as observed in mayflies (Flenner et al. 2009). However, we cannot rule out plastic cuticle responses because less than half of the predator-cued larvae achieved two moults during this experiment, limiting the opportunity to change the biomechanical properties of lamellar joints during moulting. Additionally, species differences between *E. ebrium* and *E. hageni* could have obscured a plastic response in cuticle thickness.

The biomechanical details of lamellar autotomy during predator–prey interactions are unknown, raising the possibility of testing biases, for example, by applying a 2 mm s^{-1} joint strain rate in our tensile testing. Lamellar joints may be strained during predation in a variety of ways (e.g., due to size differences between prey and predator), and the range of conditions under which autotomy operates (e.g., temperature) may also influence performance. However, these effects seem minor compared to the biomechanical effects elicited by dragonfly predation cues because autotomy threshold differences persisted over different strain rates, studies, and possibly the two species examined here. For example, Gleason et al. (2014) detected a relationship between joint diameter and peak breaking force using a slower strain rate of 10 mm min^{-1}.

Furthermore, other properties may also contribute to plasticity in peak joint breaking force, especially because changes in cuticle thickness were negligible. For example, protein composition of cuticles (Hopkins and Kramer 1992), the tracheae that cross through the lamellar joint, or joint cross sectional shape may also influence how joints respond to breaking stress. Our focus on ‘passive’ joint rupture in freshly killed larvae also ignores the possibility of active mechanisms that control lamellar autotomy (e.g., Clarac et al. 1971; McVean 1973; Bellairs and Bryant 1985). Lastly, we do not know whether lamellar plasticity is reversible with larger and stronger joints induced by removing pre-existing dragonfly predator cues or by adding fish predator cues. The full range of plastic responses to the presence and absence of dragonfly and fish cues will be required in order to evaluate whether plasticity in lamellar autotomy is adaptive.

Testing an adaptive hypothesis also requires that variation in autotomy threshold influences fitness (Arnold 1983). We assume that weakened lamellar joints increases survival by allowing prey to break away from larger predatory larvae of dragonflies or conspecifics during the post-contact resistance phase of a predator–prey interaction (Robinson et al. 1991a; Stoks et al. 1999). However, crypsis and pre-contact behaviour also function to avoiding predators (e.g., Cooper and Vitt 1991; Gyssels and Stoks 2005) and so the contribution made by autotomy relative to other anti-predator traits needs further study. Nevertheless, these uncertainties do not undermine our findings of functional plasticity in autotomy in response to predatory dragonfly cues.

Predator cues elicited other indirect responses that influenced larval fitness. Non-consumptive predator effects on prey behaviour, growth, life history, and survival can exceed direct mortality effects (Pressier et al. 2005; McCauley et al. 2011). Consistent with prior studies, mortality was increased and growth was reduced in larvae from the predator relative to control treatments (e.g., McPeek et al. 2001; McPeek 2004; Stoks 2001; Stoks et al. 2005; McCauley et al. 2011). Indirect mortality effects could arise from physiological responses to stress that influence energy intake and allocation (Brodin et al. 2006; Stoks 2001), assimilation (Sapolsky 2002; Slos and Stoks 2008), increased stress (Sorensen et al. 2003), and compromised immune response (Slos and Stoks 2008). Current stress theory focuses on organismal energy balance, where energy used to recover from stress is removed from normal activities (Sokolova et al. 2012). Reallocation could have contributed to smaller and weaker joints in the predator treatment larvae here (e.g., Flenner et al. 2009).

Given current stress theory (Sokolova et al. 2012), differential mortality to predator cues does not readily account for the differences in joint morphology and autotomy performance. For example, predator treatment larvae with larger and stronger joints would have had to die at higher rates than those with smaller and weaker joints. However, there is no reason to expect this since predator cues generally depress food intake, increase stress, reduce growth, and increase mortality as noted above. Individuals least susceptible to predator indirect effects are more likely to survive and to develop normally and so should have lamellae more similar to control larvae.

Autotomy as an inducible defense

We modeled an optimal autotomy threshold that balances the probabilities of autotomy, mortality under predation risk, and the costs of autotomy (C) (supplementary material 1). The model suggests that uncertainty in predation risk can be resolved by prey adjusting the threshold to match local predator conditions (Benard 2004; Johansson and Stoks 2005). The model is not explicitly genetic or developmental. Thus, it cannot explicitly distinguish adaptive evolutionary divergence in the autotomy threshold between populations that persistently experience alternate predator conditions from adaptive plastic developmental responses to heterogeneity in predation cues. The later case would constitute a novel inducible defense mechanism by prey that has not been formally considered to date (Benard 2004; Johansson and Stoks 2005).

The model also expands our understanding of how the costs relative to benefits of autotomy might shape microevolutionary or plastic developmental responses. Grasping predators generate selection for lower autotomy threshold. However, the threshold also regulates the risk of incurring costs in direct proportion to the probability of autotomy (Fig. 1). Thus, the threshold mediates a trade-off between the probabilities of avoiding mortality and incurring costs. Under risk from grasping predators, one solution to this trade-off is to adjust the threshold upwards so that the probability of autotomy (p) is reduced by an amount $p = C/(1 + C)$, where C is the fitness cost arising from reduced organismal performance due to absence of an appendage. In the absence of predators, a higher threshold is favoured because it avoids the costs of accidental autotomy. Comprehensive estimates of the costs of autotomy theoretically could be used to predict how much the autotomy threshold will change under a particular predator treatment, although this is not yet possible. However, the 29% reduction in peak breaking force in the dragonfly predator relative to the no-predator control treatment here suggests that the costs of autotomy are likely high in larval *Enallagma*.

The plastic response to predatory dragonfly cues observed here also provide a proximal mechanism for variation among natural populations (Cooper et al. 2004; Bose and

Robinson 2013). However, two key pieces of evidence are required to evaluate whether plasticity in autotomy represents an adaptive inducible defense. First, the lower autotomy threshold induced by predatory dragonfly cues would have to enhance larval survival under predation from dragonfly larvae. Second, damselfly larvae would also have to adjust their autotomy threshold upwards in response to fish cues in order to reduce autotomy costs (Flenner et al. 2009). More generally, inducible defense predicts that rates of plastic autotomy responses should be matched to temporal heterogeneity in mortality risk, yet we know almost nothing about the patterns of heterogeneity in mortality risks for most species that express autotomy. Hence, while we have resolved a key uncertainty about whether autotomy can be plastic, we have only just begun to consider whether such plasticity might have evolved as an inducible defense.

Acknowledgements J. Gleason advised on tensile testing and SEM, and A. Brown, V. Corbin, N. Deveau, C. Rosa, E. Matczak, M. Tregenza, J. Seery, and J. Stiles assisted field sampling or provided for animal care during the experiment. We are grateful for discussions with R. McLaughlin, A. McAdam, C. Axelrod and D. Gislason that assisted model development, and to comments from two anonymous reviewers that improved the manuscript. This study was supported by Discovery Grants from the Natural Sciences and Engineering Research Council of Canada [RGPIN-2014-04455 to BWR, and RGPIN-2016-04967 to DSF].

Compliance with ethical standards

Conflict of interest The authors declare no conflicts of interest.

Ethical approval Animals were cared for in accordance with animal use and welfare standards administered by the University of Guelph under Canadian government guidelines (UAREB No. 1500).

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