

# How does the timing of weapon loss influence reproductive traits and trade-offs in the insect *Narnia femorata*?

E.V.(Ginny) Greenway<sup>1,2</sup>, Emily Angelis<sup>1</sup>, Christine W. Miller<sup>1</sup>

<sup>1</sup>Entomology and Nematology Department, University of Florida, Gainesville, FL, United States

<sup>2</sup>School of Biological Sciences, University of East Anglia, Norwich, Norfolk, United Kingdom

Corresponding author: School of Biological Sciences, University of East Anglia, Norwich, Norfolk NR4 7TJ, United Kingdom. Email: [G.Greenway@uea.ac.uk](mailto:G.Greenway@uea.ac.uk)

## Abstract

A longstanding goal of evolutionary biology is to understand among-individual variation in resource allocation decisions and the timing of these decisions. Recent studies have shown that investment in elaborate and costly weapons can result in trade-offs with investment in testes. In this study, we ask the following questions: At what point plasticity in resource allocation to these different structures ceases during development, if at all? Furthermore, can individuals tailor their reproductive behavior to accompany structural changes? We experimentally addressed these questions in the insect *Narnia femorata*, quantifying resource reallocation across development for the first time, using a phenotypic engineering approach. To investigate whether allocation plasticity diminishes throughout ontogeny, we induced weapon loss at a range of different developmental stages and examined subsequent testes mass and reproductive behavior. We found that relative testes mass increased as weapon investment decreased, implying a direct trade-off between testes and weapon investment. However, autotomy postadulthood ceased to induce larger testes mass. Intriguingly, losing a weapon while young was associated with extended adult mating duration, potentially enabling compensation for reduced fighting ability. Our results highlight the importance of examining the ontogeny of trade-offs between reproductive traits and the flexibility of the relationship between reproductive morphology and behavior.

**Keywords:** sexual selection, trade-off, autotomy, insect weapons, phenotypic plasticity

## Introduction

Male–male competition for mating opportunities has driven the evolution of elaborate sexually selected weapons, ranging from the enormous antlers of stags to the exaggerated limbs of some insect species (Emlen, 2008). These sexually selected weapons have evolved for use in physical contests between males for access to females (McCullough et al., 2016). However, the rivalry between males often does not end there, continuing into the postcopulatory phase in the form of sperm competition (Birkhead & Hunter, 1990; Parker, 1979). This poses a potential challenge: producing and maintaining both precopulatory weapons and postcopulatory traits is likely demanding. Given that animals have finite resource budgets, investment in one trait may come at the cost of another, leading to a trade-off (van Noordwijk & de Jong, 1986; Zera & Harshman, 2001). Indeed, negative correlations between investment in precopulatory traits and primary reproductive traits (e.g., testes) have been uncovered in multiple systems (e.g., Dines et al., 2015; Durrant et al., 2016; Klaus et al., 2011; Lüpold et al., 2014; Simmons & Emlen, 2006; Simmons et al., 2017). Experimental ablation of horn structures during development in beetles leads to the growth of larger testes (Simmons & Emlen, 2006), as does the removal of a hind limb weapon in juvenile true bugs (Joseph et al., 2018; Somjee et al., 2018a). Although these manipulations illustrate that trade-offs exist between these traits, they

also implicitly demonstrate that resource allocation between pre- and postcopulatory traits is flexible and dynamic, at least during juvenile life stages. Yet, our knowledge of the extent of developmental plasticity in resource allocation is incomplete. Additionally, the mechanisms underlying resource reallocation across pre- and postcopulatory traits remain unclear.

Although reproductive morphology and physiology may be somewhat developmentally constrained in species with determinate growth, behavior is likely to be far more flexible (Bretman et al., 2011). Behavioral flexibility provides individuals with a means to compensate for changes in morphology, including weapon loss. Indeed, alternative reproductive strategies are characterized by divergent pre- and postcopulatory investment paired with behavioral strategies that maximize the reproductive payoffs of their respective phenotypes (Gage et al., 1995; Gross, 1996; Puniamoorthy et al., 2012). Males that prioritize investment in postcopulatory traits typically expend more in each mating event they secure to increase their chances of fertilization success (Taborsky & Brockmann, 2010), via extended mating durations and increased sperm transfer (Filice & Dukas, 2019; Okada et al., 2010). In the other direction, individuals that have been phenotypically engineered to produce less sperm display reduced mating frequency (Sekii et al., 2013). If we experimentally manipulate relative investment in weapons versus testes, do individuals respond behaviorally to maximize the pay-off from the

combination of pre- and postcopulatory traits they end up with? In particular, can individuals that have lost a weapon compensate behaviorally for their limited precopulatory competitive ability when it comes to mating?

In this study, we address these unanswered questions in the leaf-footed cactus bug, *Narnia femorata*, an insect in the family Coreidae and the order of true bugs, Hemiptera. Males of this species invest in enlarged hind limbs that they use to kick and grapple with each other in contests (Nolen et al., 2017). Although these weaponized limbs are central to securing competitive and mating success, individuals can readily autotomize them to evade predation attempts and entrapment (Emberts et al., 2016, 2018). Leaf-footed bugs are hemimetabolous, developing through five juvenile instars between hatching and eclosion to adulthood, and unlike in other systems, they do not regrow their dropped limbs (Emberts et al., 2016). With each juvenile instar, they develop increasingly large hind limbs, with broadened femurs and tibial flags (Vessels et al., 2013). At eclosion to adulthood, these weaponized limbs then become fixed in external size. Juvenile limb autotomy (at the fourth instar) in this species is accompanied by a boost in relative testes mass (Joseph et al., 2018; Miller et al., 2021), suggesting that a resource allocation trade-off exists between these two metabolically expensive and condition-dependent traits (Greenway et al., 2020; Sasson et al., 2016). However, until now, this weapon–testes trade-off has only been examined after autotomy at a single juvenile time point, and the underlying mechanism behind the reallocation response is unexplored.

We first set out to investigate how the timing of autotomy influences reallocation to testes mass and begin to test the mechanistic basis of this response. If resources allocated to testes and weapon growth are drawn from the same pool and directly trade-off, we predicted a positive linear relationship between the amount of leg mass we prevented a bug investing in and the size of their relative adult testes mass. By removing the hind leg of a juvenile, we effectively blocked off investment to this body part, freeing up resources that can be deployed to the development of other traits. Removing a limb later in development, after many of the costs involved in producing that limb have already been expended, would presumably result in a proportionally smaller quantity of available resources to reallocate to testes mass. Alternatively, if autotomy acts as a trigger to switch investment to postcopulatory traits to boost sperm competition, then we predicted the size of the limb removed would not correlate with relative testes mass size.

We then asked whether autotomy is accompanied by changes in mating behavior, which may enable males to capitalize on the mating opportunities that may arise. Given that autotomized males have reduced chances of accessing mates via male–male competition (Emberts et al., 2018), we predicted that they would invest more time in each mating they engaged in, extending copulations to increase the chances of fertilization success.

## Methods

### Husbandry

Individuals used in both experiments were laboratory-reared offspring from wild-caught *N. femorata* parental pairs collected from Camp Blanding, FL. Clutches produced by the

parental pairs were separated and kept in small family groups (5–13 individuals per 32-oz clear plastic container) on their natural diet: prickly pear cactus (*Opuntia mesacantha* subsp. *lata*) with ripe fruit throughout their first three instars. Once juveniles reached the fourth instar, we transferred them into their own individual 32-oz container with a single potted prickly pear cactus with ripe fruit. We randomly assigned an individual's experimental type, treatment type, and a unique number identifier. Parental pairs and clutches were kept in Percival Scientific incubators at 28°C under a 14:10 L:D cycle. Once experimental individuals reached the fourth instar, they were transferred to a rearing room lit with T5 HO fluorescent bulbs on a 14:10 L:D cycle. Conditions within individual containers were kept consistent at 30–35°C and 40%–60% humidity, and bugs were checked daily.

### Experiment 1: Effect of autotomy timing on testes investment

Each *N. femorata* nymph was randomly assigned to one of five autotomy treatments upon reaching the fourth instar: autotomy at either the (a) fourth instar ( $n = 35$ ), (b) fifth instar ( $n = 37$ ), (c) early adulthood (2–3 days after emerging,  $n = 32$ ), (d) 14 days after adult eclosion (i.e., at sexual maturity,  $n = 32$ ), or (e) an unmanipulated control treatment ( $n = 37$ ). We induced autotomy by immobilizing the left hind femur of experimental individuals with reverse-action forceps while their tarsi were in contact with a piece of wood for grip and, if necessary, gently brushed them with a paintbrush to encourage them to self-autotomize. Autotomized limbs were then frozen at  $-20^{\circ}\text{C}$  for imaging and subsequent weighing.

### Quantifying morphology and testes mass

We kept all males in individual cups provisioned with ripe fruit over the course of the experimental period. Once males reached sexual maturity (14–16 days after adult enclosure), we froze, imaged, and measured them. We then dissected the testes of each individual and preserved them and the remaining body separately in 70% ethanol. Each male's testes and hind leg(s) plus their body and four remaining legs were placed into separate preweighed aluminum foil boats and then dried for 72 hr at  $70^{\circ}\text{C}$  before being weighed to the nearest microgram using a Mettler Toledo XP6 microbalance.

### Experiment 2: Effects of autotomy on mating behavior

Upon eclosion to fourth instar, we assigned nymphs to either a control or autotomy treatment. As in Experiment 1, we induced autotomy by gripping nymphs by the left hind femur with reverse-action forceps while in contact with a piece of wood, enabling their remaining limbs to gain traction during the process. Control bugs were subjected to a sham procedure, in which their hind femur was gripped for around a second before release following Emberts et al. (2017). All nymphs were then housed in individual plastic containers containing a cactus pad and ripe cactus fruit and checked daily.

Once they reached adulthood, they were sexed and left to reach sexual maturity (14–21 days) before being entered into behavioral trials. As mating behavior is a product of interactions between both male and female phenotypes, we included both autotomized males and autotomized females alongside control individuals. Behavior trial treatments consisted of the following fully factorial combinations of randomly paired

unrelated individuals: (a) control male–control female ( $n = 27$ ), (b) control male–autotomized female ( $n = 30$ ), (c) autotomized male–control female ( $n = 24$ ), and (d) autotomized male–autotomized female ( $n = 25$ ). This design enabled us to parse out male behavioral responses to their own autotomy status from responses to their partner's autotomy status.

We continuously observed pairs in a clear plastic container with cactus and fruit for a 3-hr period and recorded the frequency of male mounting attempts on their female partners, genital contact, copulations, alongside the latency to mount and mate and copulation duration. At the end of the behavior trial, we separated individuals and euthanized them via freezing, before measuring their pronotum width (a proxy for body size) using Mitutoyo digital calipers.

### Statistical analysis

All statistical analyses were performed in R v3.5.0 (R Core Team, 2018). To test for the effects of autotomy treatment on testes mass in Experiment 1, we used the *lme4* package to fit a linear model with testes mass as a continuous normally distributed dependent variable and treatment category and body mass as factors. Post hoc analyses were carried out using the *multcomp* package, correcting for multiple testing using single-step adjusted  $p$ -values.

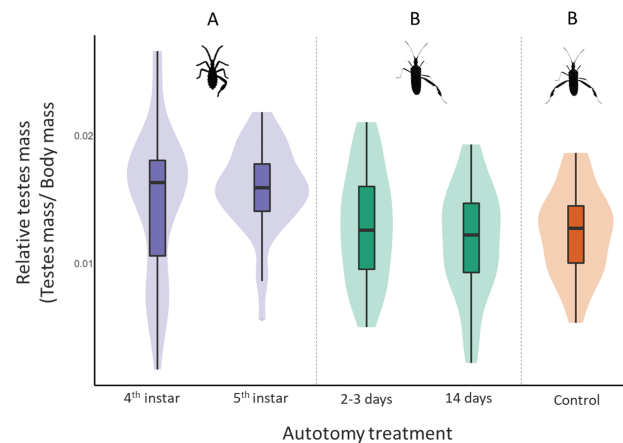
We generated a metric of hind leg mass investment "saved" for each experimental insect by subtracting the dry mass of their autotomized limb from the dry mass of their fully grown adult hind limb. We calculated this for the 103 individuals that we had both autotomized and fully grown limb dry mass measurements across treatments and then incorporated this value as a third predictor in subsequent analysis. Put another way, this calculated metric captured the resources, and we prevented these individuals from investing in growing a second full-size hind limb, which were then theoretically freed up to reinvest in the growth of other structures such as testes. To establish the validity of this metric, we compared the fully grown single hind limb mass of all autotomized males with the mean hind limb mass of intact control insects. We found no significant difference between the two, indicating that autotomy did not alter the growth and investment of the remaining limb (see Results). Thus, the remaining limb appears to be an effective proxy for the final mass of the autotomized limb had it been able to fully develop.

To analyze the results of Experiment 2, we used a generalized linear model to examine predictors of mating duration. We included male autotomy status and pronotum width, and female autotomy status and pronotum width as factors and used a quasi-Poisson distribution to account for overdispersion. To assess whether mating duration constituted a stable phenotype, we calculated how repeatable it was within pairings, which we observed mating more than once using the *rptR* package (Nakagawa & Schielzeth, 2010). Data were uploaded to Dryad and are available at <https://doi.org/10.5061/dryad.p8cz8w9vk>.

## Results

### Experiment 1: Influence of autotomy timing on testes investment

We detected a significant effect of autotomy timing on relative testes mass ( $F = 3.207$ ,  $df = 4$ ,  $p = .015$ , Figure 1). A post hoc pairwise analysis comparing each of the treatments revealed that individuals autotomized at the fifth instar had

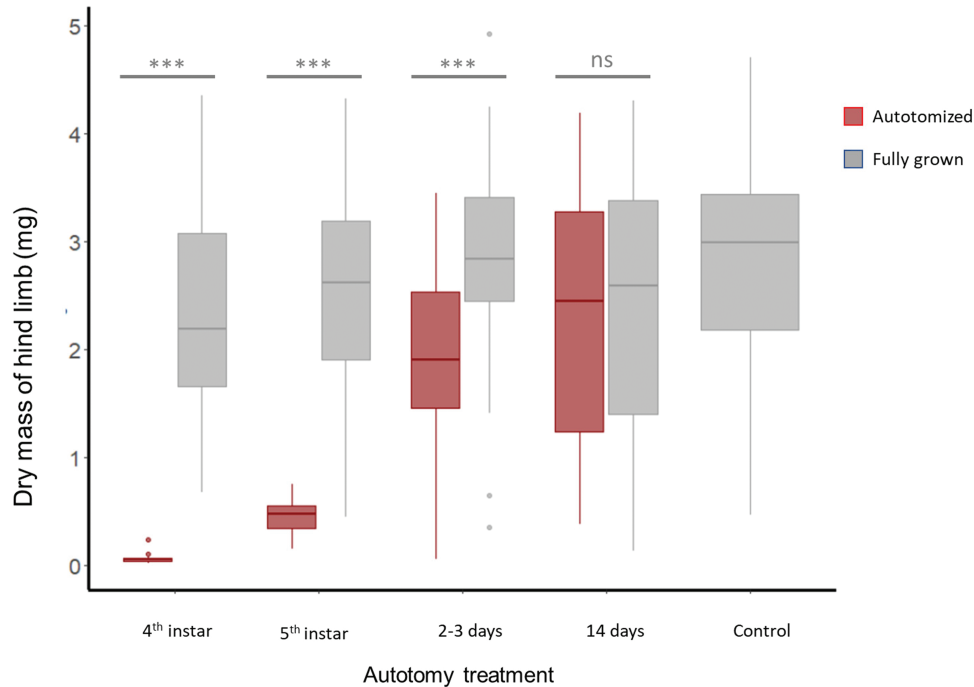


**Figure 1.** The relationship between autotomy timing and relative testes mass (shown as testes mass divided by body mass for visualization purposes). Letters between groups denote statistically significant differences at the  $p < .05$  level.

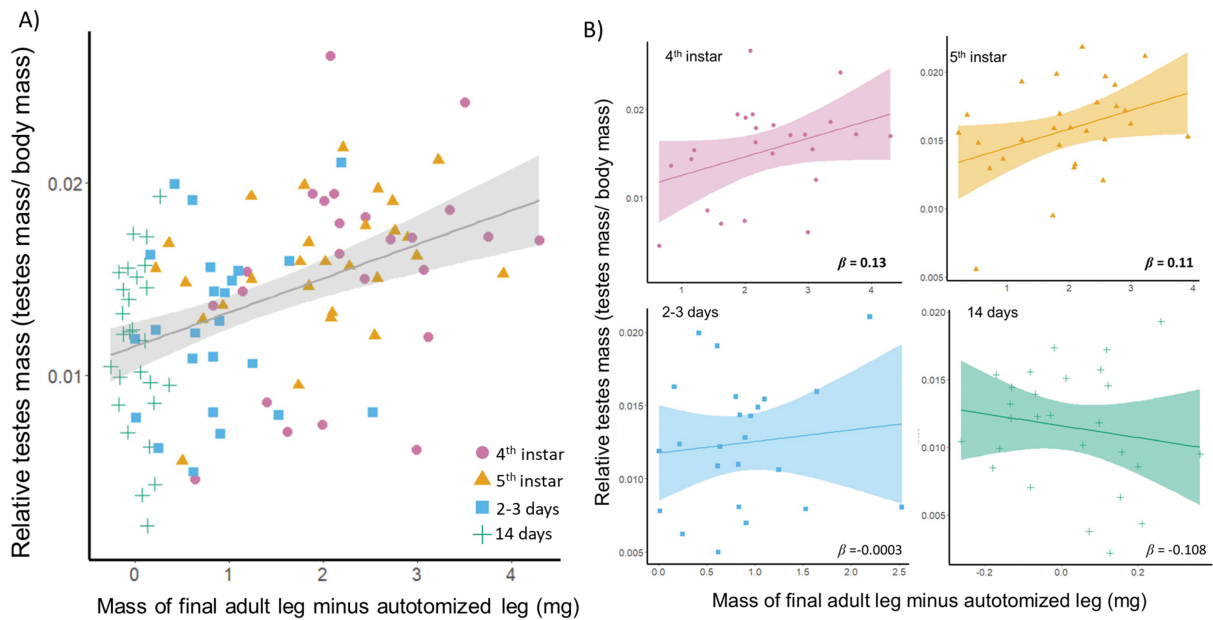
larger testes than those autotomized as sexually mature adults ( $t = -3.536$ ,  $p = .005$ ) and those left unmanipulated ( $t = -2.843$ ,  $p = .04$ ). Differences between all other treatment groups were nonsignificant. As anticipated, body mass was highly correlated with testes mass ( $F = 97.88$ ,  $df = 1$ ,  $p < .001$ ) and was therefore included as a covariate in all subsequent analyses. To establish whether eclosion to adulthood constituted a critical threshold in testes reallocation ability, we then pooled treatments into juvenile and adult stages. Again, the life stage at which autotomy occurred influenced testes mass ( $F = 6.7$ ,  $df = 2$ ,  $p = .002$ ); males autotomized prior to adulthood developed significantly larger testes for their body size than individuals autotomized as adults ( $t = -3.33$ ,  $p = .0029$ ) or those left intact as a control ( $t = -2.777$ ,  $p = .017$ , Figure 1).

Autotomy treatment had no significant impact on the mass of the remaining adult hind limb, which did not differ from the equivalent hind limb of control individuals ( $n = 172$ ,  $df = 4$ ,  $F = 1.751$ ,  $p = .141$ , Figure 2). As such, the mass difference between the autotomized hind limb and the final adult hind limb served as an effective proxy for the mass investment "saved" via autotomy (see Methods). Using this difference as a proxy for resource investment saved, we found that the mass of hind leg tissue *not* grown was positively correlated with testes mass ( $\beta = 0.059$ ,  $F = 14.19$ ,  $p = .0003$ , Figure 3A). Together, body mass and the amount of leg mass an individual "saved" through autotomy explained 51% of the variance in autotomized male testes mass (Figure 3A). Males that were autotomized earliest in development "saved" the largest amount of leg mass investment, whereas those that were autotomized as sexually mature adults "saved" negligible mass investment. Intriguingly, the hind limbs autotomized by 2- to 3-day-old males were significantly lighter than their fully grown adult limbs (Figure 2,  $F = 16.04$ ,  $df = 1$ ,  $p < .001$ ), suggesting that further investment occurs in cuticle and/or muscle during this period of adult maturation.

Upon closer examination, the overall positive association between mass "saved" and relative testes mass was driven by changes induced in fourth- and fifth-instar individuals (fourth instar:  $\beta = 0.13$ ,  $t = 3.430$ ,  $p = .0025$ ; fifth instar:  $\beta = 0.11$ ,  $t = 4.483$ ,  $p = .0001$ , see Figure 3B). Once individuals reach



**Figure 2.** Autotomy had no impact on the mass of the remaining fully grown adult hind limb (gray) across all treatment groups relative to the hind limbs of intact control individuals. The mass of the autotomized leg (red) increased across instars but was significantly lower than the fully grown adult leg except when removed at 14 days. \*\*\*Significant pairwise differences at the  $p < .001$  level between the autotomized and remaining adult limb mass.



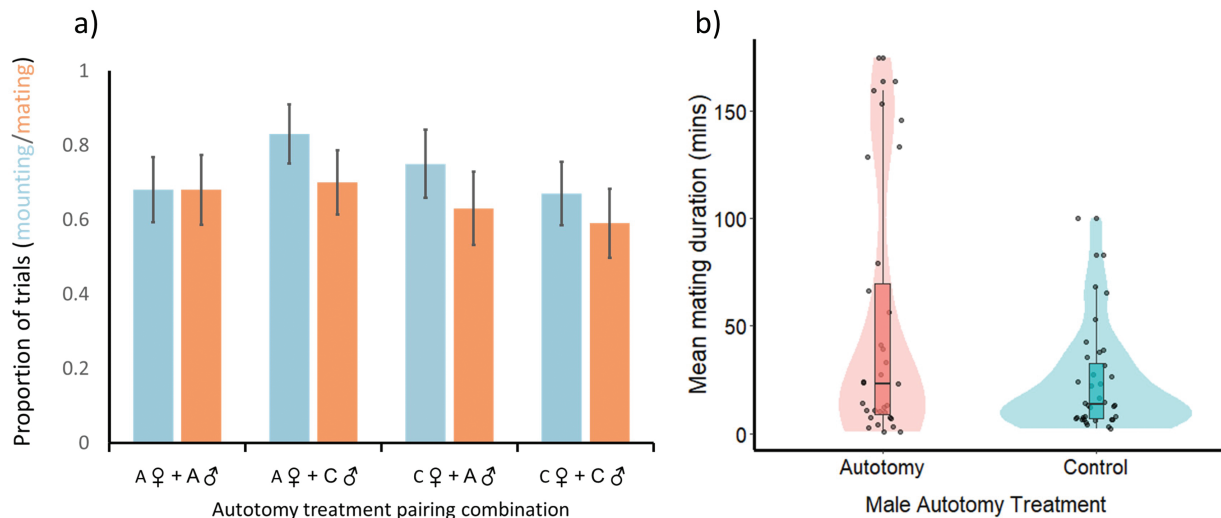
**Figure 3.** (A) The overall relationship between the mass investment “saved” (i.e., mass of adult hind leg minus mass of autotomized leg) and relative final testes mass, shown with linear regression and shaded 95% confidence intervals for visualization purposes. (B) Relationships between the mass investment “saved” (i.e., mass of adult hind leg minus mass of autotomized leg) and relative testes mass across the four experimental treatments. Slope values were calculated from linear models with testes mass as the dependent variable and body mass as a covariate. Values in bold denote slope values that differ significantly from zero at the  $p < .05$  level. Sample sizes across treatments vary between  $n = 21$  and  $n = 25$ .

adulthood, we observed no significant effects of the mass of tissue “saved” via autotomy on testes mass, when controlling for body size (2- to 3-day adults:  $\beta = -0.0003$ ,  $t = -0.009$ ,  $p = .99$ ; 14-day adults:  $\beta = -0.108$ ,  $t = -0.721$ ,  $p = .478$ , Figure 3B).

**Experiment 2: Effects of hind limb loss on mating behavior**

We found that male individuals with hind limbs autotomized as juveniles mated for significantly longer duration

with females regardless of whether females were autotomized or intact (LRT,  $\chi^2 = 12.44$ ,  $df = 1$ ,  $p < .001$ , Figure 4B). What’s more, this longer mating duration associated with male autotomy was significantly repeatable in pairs that copulated at least twice during the 3-hr trial:  $R = .21$ , 95% Confidence Intervals (CI) = (0.04, 0.357),  $p = .0019$ . The mating duration was also positively associated with female body size (Likelihood Ratio Test [LRT],  $\chi^2 = 6.22$ ,  $df = 1$ ,  $p < .0126$ ).



**Figure 4.** (A) The proportion of trials in which males mounted (blue) and mated (orange) with females across four different autotomy and control pair combinations  $\pm 1$  SE and (B) the impact of male autotomy on mean mating duration.

We found that the autotomy treatment did not appear to affect any other measured aspects of mating behavior; rates of mounting and mating did not differ across the four possible pairing combinations ( $\chi^2 = 0.24$ ,  $df = 1$ ,  $p = .622$ , Figure 4A). Across treatments, 78 of the 106 males (73.6%) mounted the female they were paired with during the mating trial and 69 of these 106 males (65.1%) subsequently succeeded in mating. We found no effect of either male or female treatment (autotomy or control) on average latency to first mount or average latency to first mate.

## Discussion

In this study, we demonstrate that the trade-off between these insects' precopulatory weapons and their testes is developmentally time sensitive and only manifested if limb loss occurred in the juvenile stage. Induction of limb loss once individuals reached adulthood did not generate a boost in relative testes mass. For the first time, to our knowledge, we were also able to directly track potential resource reallocation by blocking off investment to a body part via autotomy at different time points and calculating a proxy of tissue investment saved. We found a positive linear relationship between the amount of mass a bug "saved" and the size of their relative adult testes mass. Intriguingly, the loss of a hind limb as a juvenile was also accompanied by a behavioral change; autotomized males mated for a significantly longer duration, providing them with a potential complementary pathway to increased postcopulatory success. As autotomized males' precopulatory chances are slim (Emberts et al., 2018), investing heavily in sperm production through enlarged testes may enable them to maximize their chances of siring offspring if they do manage to secure a mating opportunity.

Autotomy may drive the morphological and behavioral plasticity by (a) acting as a stimulus to switch to a predominantly postcopulatory competitive strategy or (b) a closure of a resource allocation channel, freeing up resources to reinvest directly elsewhere, or both. The question of why males that lose a limb postadulthood do not invest in relatively larger testes remains. This limited plasticity in response to autotomy may be for one of two non-mutually exclusive reasons:

a reduction in the resources available to reinvest and a loss of plasticity in adulthood.

## Resource availability

First, investment in testes mass may be directly traded off against investment in hind leg mass. As a result, experimental individuals that have invested in growing an adult limb are unlikely to make any investment savings if they drop it after eclosing to their final adult form. They have already built an enlarged weapon structure that will not grow larger in external size during adulthood. In support of this hypothesis, we observe a significant linear relationship between hind leg weapon mass saved and relative testes mass in the insects autotomized in the fourth and fifth instars. This implies the existence of a direct trade-off between the two tissues, and that resources used to grow each structure are drawn from the same shared pool.

Importantly, investment in a hind leg weapon is not limited to building the external structure. These insects also incur maintenance costs and must support the ongoing metabolic activity of this enlarged hind limb with its internal muscle and high density of mitochondria (Greenway et al., 2020; Somjee et al., 2018b). Notably, the left hind legs removed through autotomy early in adulthood were considerably lighter than their fully grown right limb. This species and others lay down endocuticle for at least the first few weeks of adulthood, and internal tissue deposition in this weapon does not stop at eclosion (Lees, 1952; Neville, 1965; Hill & Goldsworthy, 1968; Wang et al., 2018; Greenway et al., in preparation). This suggests that insects that lost a limb within the first 3 days of adulthood partially saved additional cuticle investment as well maintenance costs for the last 10 or so days of the experiment. However, these individuals did not differ significantly in their relative testes mass when compared with insects that were autotomized 14 days into the experiment, having grown and maintained two full-size hind limbs. Perhaps the costs of tissue investment saved from adulthood onward were insufficient to generate a detectable boost in relative testes mass. Alternatively, this lack of response suggests that individuals may be restricted in their developmental

flexibility beyond adult eclosion, rendering them unable to reallocate any resources freed up via autotomy.

### Timing/loss of plasticity

Although the amount of tissue saved is necessarily conflated with the developmental time point at which we induced autotomy (as hind limb size increases with each developmental instar), we looked for patterns in relative testes size within treatments to try and parse apart these two factors. Individuals autotomized during the fourth and fifth instars display positive linear relationships between mass “saved” and relative testes mass. However, adults with comparable potential mass savings to be had (with up to 2.5-mg difference between their autotomized and final leg) showed no such increase in testes mass, and we detected no correlation between the two at this life stage. This lack of response may be attributed to developmental canalization, which could restrict these insects’ ability to alter investment in testes mass beyond their fifth instar. Similarly, in species with minor and major male morphs, there may be a threshold or switch point in development at which individuals diverge down different developmental trajectories, prioritizing either pre- or postcopulatory traits (Emlen, 1994; Emlen & Nijhout, 1999; Taborsky & Brockmann, 2010). In male dung beetles, this window of sensitivity for prioritizing weapon growth is a narrow period near the end of the third larval instar, during which topical hormone application can induce the development of a major morph phenotype (Emlen & Nijhout, 1999; Nijhout, 2003). The timing of allocation to weapons versus testes in hemimetabolous insects, which molt through successive instars, is unclear. Soft internal tissue, such as reproductive organs, typically continues to grow and develop well into adulthood when organisms hit sexual maturity (Dumser, 1980; Hayes & Wall, 1999). However, architectural changes in testes mass (like those associated with autotomy in the fourth instar in this species; Cavender et al., 2021) may not be possible past a certain developmental time point (Dumser, 1980). As mentioned above, certain elements of the exoskeleton are fixed upon adulthood, whereas others remain dynamic and continue to require investment throughout adult life. Therefore, the stages at which these traits are sensitive to external environmental factors may differ, leading to complex changes in directionality and timing of resource reallocation among these pre- and postcopulatory traits (McDermott & Safran, 2021; Riska, 1986).

### Compensatory behavior

What use are larger testes without a corresponding behavioral shift? To capitalize on their increase in relative testes mass, autotomized males appear to change at least one aspect of their mating behavior. Males missing a hind limb increased their time spent mating with females, potentially compensating for their lost weapon. The proximate mechanism for the increase in testes mass that autotomized males experience appears to be an increase in mitotic divisions in spermatogonia, which in turn likely increases the number of spermatocytes and sperm cells produced (Cavender et al., 2021). A previous study in *N. femorata* revealed that pairings involving autotomized males produced significantly more offspring than their intact counterparts (Joseph et al., 2018). We do not yet know how mating duration relates to sperm transfer, but testes mass is linked to fertilization success in this species (Greenway et al., 2020), and increased mating duration may be a contributor to the boost in offspring production that

autotomized individuals experience. In principle, mating for longer may enable autotomized males to capitalize on their enhanced sperm production abilities and transfer larger ejaculates, which can outcompete those of intact males for access to fertilization (Engqvist & Sauer, 2003; Parker et al., 1999; Pilastro et al., 2007). Indeed, males also displayed longer mating durations when paired with larger females in this study, supporting the interpretation that mating duration represents a form of male investment (Parker et al., 1999).

Mate guarding can be characterized by prolonged matings; thus, it is possible that the increased mating duration by autotomized males in this study serves to reduce the access of rival males to fertilization opportunities (Alcock, 1994; Carroll, 1991; Mclain, 1989). Although we cannot rule out the possibility that females may influence copulation duration, extended mating durations were only observed in pairings in which males were autotomized and were significantly repeatable within pairings. Therefore, this mating behavioral difference appears to be male associated and may help compensate for their missing weapon. By staying in copula for longer, a male can prevent a female from remating before she oviposits and increase the likelihood that his sperm is used to fertilize her eggs (Alcock, 1994). Although autotomized males only mate for around 15 min longer than intact males, this could still confer a fitness benefit. For context, there is limited evidence that wild adults survive beyond 1 month in the wild, and observed mating rates under seminatural conditions are low; males mate with zero to four females over a 5-day period (Cirino & Miller, 2017, Greenway & Miller, in preparation). Given autotomized males have even lower chances of securing mating opportunities due to their missing precopulatory weapon, extended mating durations could have significant payoffs in terms of sperm transfer and reproductive success (Emberts et al., 2018). Behaviors such as mate guarding, mating duration, and broader mating investment are typically plastic and highly context dependent, especially when compared with developmentally constrained physiology traits such as testes size (Bretman et al., 2011; Parker, 1990; Shandilya et al., 2018; Simmons, 2001). As such, investigating the extent to which these insects adjust aspects of their mating behavior in response to autotomy at different developmental time points is a logical next step of inquiry.

Overall, we found evidence of dynamic allocation between pre- and postcopulatory traits and a complex interplay between morphology and behavior, which come together to shape each individual’s reproductive phenotype. Individuals appear to be able to redirect resources to testes growth when experimentally prevented from investing in a precopulatory weapon, but this phenotypic plasticity diminishes upon adulthood. Although the proximate drivers and timing of such trade-offs have previously been focused on in holometabolous insects, given their fixed resource budget and rapid development phase as pupae (Emlen, 2001; Moczek & Nijhout, 2004; Nijhout & Emlen, 1998; Tomkins et al., 2005), clearly similar patterns exist in hemimetabolous insects and potentially other animals that feed continuously throughout development. Sexually selected traits represent a fertile testing ground for further empirical exploration of the ontogeny of life history trade-offs (Lande, 2019; McDermott & Safran, 2021; Riska, 1986).

### Data availability

Data are available via Dryad at <https://doi.org/doi:10.5061/dryad.p8cz8w9vk>.

## Author contributions

E.V.G. and C.W.M. conceived the idea for this research and designed the methodology; E.V.G. and E.A. collected the data; E.V.G. and E.A. analyzed the data; E.V.G. and C.W.M. led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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