

# Experimental manipulation reveals a trade-off between weapons and testes

U. SOMJEE\* , C. W. MILLER\*, N. J. TATARNIC†‡ & L. W. SIMMONS†

\*Entomology and Nematology Department, University of Florida, Gainesville, FL, USA

†Centre for Evolutionary Biology, School of Biological Sciences, University of Western Australia, Crawley, WA, Australia

‡Department of Terrestrial Zoology, Western Australian Museum, Welshpool, WA, Australia

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## Abstract

Theory predicts a trade-off between sexually selected weapons used to secure mates and post-copulatory traits used to maximize fertilization success. However, individuals that have a greater capacity to acquire resources from the environment may invest more in both pre- and post-copulatory traits, and trade-offs may not be readily apparent. Here, we manipulate the phenotype of developing individuals to examine allocation trade-offs between weapons and testes in *Mictis profana* (Hemiptera: Coreidae), a species where the hind legs are sexually selected weapons used in contests over access to females. We experimentally prevented males from developing weapons by inducing them to autotomize their hind legs before the final moult to adulthood. We compared trait expression in this group to males where autotomy was induced in the mid-legs, which are presumably not under sexual selection to the same extent. We found males without weapons invested proportionally more in testes mass than those with their mid-legs removed. Males that developed to adulthood without weapons did not differ from the mid-leg removal group in other traits potentially under pre-copulatory sexual selection, other post-copulatory traits or naturally selected traits. In addition, a sample of adult males from the same population in the wild revealed a positive correlation between investment in testes and weapons. Our study presents a critical contribution to a growing body of literature suggesting the allocation of resources to pre- and post-copulatory sexual traits is influenced by a resource allocation trade-off and that this trade-off may only be revealed with experimental manipulation.

## Introduction

Competition for mating opportunities drives the evolution of a diversity of male sexual weapons, from the tusks of elephants to the exaggerated limbs of many insect species (reviewed in Emlen, 2008). However, competition among males often continues after mating and drives the evolution of exaggerated post-copulatory sexual traits, from complex genitalia to sperm form and function (Eberhard, 2009; Simmons & Fitzpatrick, 2012). Sexually selected weapons function in mate acquisition, where males that invest more in weaponry

are often more successful in monopolizing mates. However, when females mate with multiple males, fertilization success may also depend on a male's ability to compete with the ejaculates of other males either through sperm competition (Parker, 1970; Simmons, 2001) or as females bias paternity in favour of males possessing particular ejaculate traits (Eberhard, 2009). Therefore, a male's ultimate reproductive success is determined by his success in both pre- and post-copulatory arenas of sexual selection. Understanding the ways in which males allocate limited resources to competition for reproduction before and after mating remains a fundamental question in evolutionary biology (Kvarnemo & Simmons, 2013; Simmons *et al.*, 2017).

Increased investment in post-copulatory traits can contribute to increased reproductive success in polyandrous organisms, but these traits can also be energetically

Correspondence: Ummat Somjee, Entomology and Nematology Department, University of Florida, Gainesville, FL, USA.  
Tel.: +1 (352) 273 3901; fax: +1 (352) 392 0190;  
e-mail: ummat.s@gmail.com

demanding. Increased spermatogenesis can lead to reduced lifespan (Van Voorhies, 1992), and individuals with poor nutrition may be unable to produce large testes or sustain high rates of spermatogenesis (Olsson *et al.*, 1997). In addition, investment in the production of weapons should be costly. Indeed, sexually selected weapons and ornaments are known to exhibit heightened condition-dependent expression (Cotton *et al.*, 2004; Bonduriansky *et al.*, 2012; Miller *et al.*, 2016); generally, individuals that develop sexual weapons under poor nutrient conditions have proportionally smaller weapons (*e.g.* Lewis *et al.*, 2012; Warren *et al.*, 2013; Rosenthal & Hebets, 2015). As both pre- and post-copulatory traits can be energetically demanding, males are expected to face allocation decisions when investing in one set of traits or the other. Indeed, recent theoretical models of sperm competition predict that males should trade expenditure on weapons for increased ejaculate expenditure as the risk and intensity of sperm competition increases (Parker *et al.*, 2013) a prediction which has received support from comparative analyses within and across taxa (Lüpold *et al.*, 2014; Dines *et al.*, 2015; Fitzpatrick & Lüpold, 2015; Kahl *et al.*, 2015; Simmons *et al.*, 2017). However, experimental manipulations that examine resource allocation trade-offs between weapons and testes within species are rare.

Traits that are energetically demanding to produce may compete for limited resources in a developing organism; the allocation differences between competing traits can generate reversals in expression, or 'trade-offs,' where allocation of more resources to one trait reduces the resources available to other traits (Stearns, 1989; Zera & Harshman, 2001). However, in many cases, negative correlations among traits are not detected. No correlations or even positive correlations may occur because individuals vary in their ability to acquire resources from the environment such that some individuals acquire sufficient resources to express large precopulatory weapons and large testes, whereas others might compromise one or both traits (van Noordwijk & de Jong, 1986; de Jong & van Noordwijk, 1992). Thus, if underlying trade-offs occur, these can be masked by variation in the acquisition and allocation of available resources (Reznick *et al.*, 2000; Simmons *et al.*, 2017).

To reveal resource allocation trade-offs, it is necessary to perform experimental studies where one of the traits in question can be manipulated in isolation, to reveal effects on other traits (Roff, 2002). To date, exceptionally few studies have used experimental manipulations to examine the relationship between pre- and post-copulatory traits; those that have employed an experimental approach have reported evidence of resource allocation trade-offs between sexually selected pre- and post-copulatory traits (Moczek & Nijhout, 2004; Fry, 2006; Simmons & Emlen, 2006; Joseph *et al.*, 2017). The scarcity of studies is likely a result of the difficulty in manipulating allocation to isolated traits, yet these

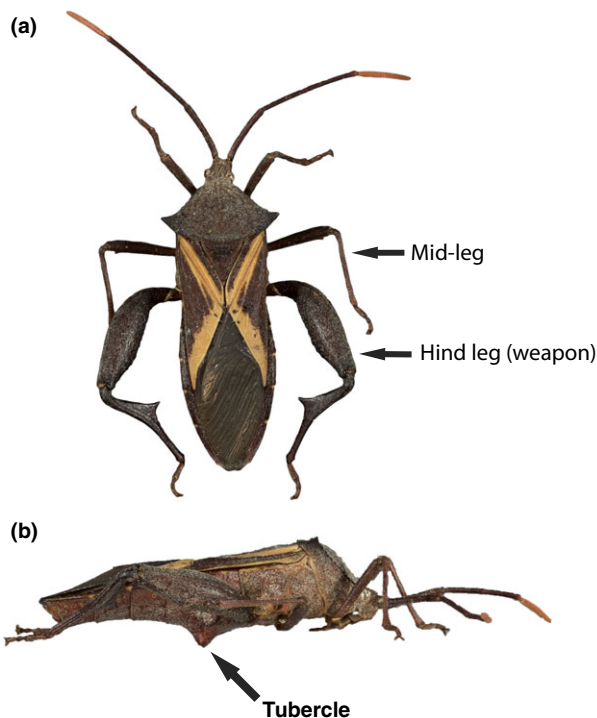
experimental manipulations remain a powerful tool for uncovering allocation trade-offs among life-history traits (Simmons *et al.*, 2017).

Here, we test the hypothesis that males trade expenditure on precopulatory weapons for post-copulatory ejaculate traits using the crusader bug, *Mictis profana* (Hemiptera: Coreidae). *M. profana* is a sexually dimorphic insect where males invest in exaggerated hind legs used as weapons over competition for mates. Hind legs can account for up to 19% of total somatic mass in adult males and are used in contests, where males wrap their legs around a competitor and perform a series of powerful kicks and squeezes (Tatarnic & Spence, 2013). The exaggerated development of male hind legs occurs primarily during the last moult to adulthood. Sexually selected weapons are often selected in concert with supportive traits that allow animals to use these weapons effectively, or enhance the function of these weapons (Miyatake, 1997). The compensatory role of supportive traits is hypothesized to drive correlational selection with weapons, resulting in integrated development among them (Cheverud, 1996; Wagner, 1996). *M. profana* possess sexually dimorphic tubercles that erupt from the lower abdomen of males, and come into direct contact with opponents during competition. These tubercles, though considerably smaller than the weapons themselves, are thought to function in concert with the hind leg weapons to enhance success in male-male contests (Tatarnic & Spence, 2013). Supportive traits can be less exaggerated than sexually selected weapons. However, changes in weapon expression can be predicted to lead to changes in the expression of supportive traits because of the close developmental integration among these traits (Cheverud, 1996; Wagner, 1996). We therefore looked for evidence of trade-offs between multiple sexually dimorphic traits in this insect.

*M. profana* undergo limb loss, or autotomy, where they eject their hind legs in response to entrapment, a feature common to many species in the family Coreidae (Emberts *et al.*, 2016). Lost limbs do not grow back in *M. profana*. To test the prediction that pre- and post-copulatory traits are subject to a resource allocation trade-off during development, we experimentally induced weapon autotomy in our treatment group before the final moult to adulthood. If males face a trade-off between allocation to weapons and testes, we predict that males that have no hind legs in which to invest at adulthood would have more resources to allocate to post-copulatory traits (testes mass, sperm storage organ volume and sperm length) relative to other traits, such as front legs or antennae. Our objective in this study was to use experimental manipulation to uncover underlying trade-offs among different pre- and post-copulatory traits which might not be revealed by examining phenotypic correlations from intact and unmanipulated individuals in the wild.

## Materials and methods

*Mictis profana* nymphs and adults were collected between 21 February and 30 March from wild populations around metropolitan Perth, Western Australia. Insects were found feeding primarily on species of *Acacia* (Fabales: Fabaceae) their native host plants (Flanagan, 1994). Nymphs found in their 3rd and 4th instar were housed individually in aerated plastic containers with a moist paper towel and provided with a diet of washed snowpeas and oranges, a diet previously documented to be sufficient for development and reproduction (Tatarnic & Spence, 2013). We kept the nymphs at a constant temperature of 29 °C with a 12-L : 12-D photoperiod. After moulting into their final instar before adulthood (5th instar), individuals were randomly allocated to one of two treatment groups: (A) hind legs removed (no weapons) (B) mid-legs removed (control for leg removal). Mid-legs in this species are shorter and much smaller than hind legs (proportional mass at 5th instar: hind legs = 10.4%, mid-legs = 3.9%). Their use in male–male conflict may be for gripping other males and surfaces, but they do not have the striking or squeezing function of the



**Fig. 1** *Mictis profana* image. *Mictis profana* male with enlarged legs modified as weapons, notice enlarged femora and tibial spines which contact opponents during combat (a: dorsal view). Males exhibit a large central tubercle, a sclerotized projection of the abdomen which is often engaged during combat with rival males (b: lateral view, photos by Nikolai Tatarnic).

exaggerated hindlimbs (Fig. 1). Thus, they are an appropriate control because they do not appear to function directly in male–male competition. We induced autotomy bilaterally (A: both hind legs,  $n = 16$ ; B: both mid-legs,  $n = 12$ ) in juveniles, resulting in an adult missing those autotomized limbs. For each limb removal, the leg was held firmly with reverse pressure forceps to induce the insect to release the leg. We then reared the juveniles to adulthood in individual containers. Adults were measured and dissected 17 days after their final moult: wild-caught *M. profana* were ready to mate at this age (U. Somjee pers. obs), and other coriids are ready to mate and have fully developed sexual traits by this age (Somjee *et al.*, 2015).

For adults in the treatment and control groups, we measured fresh weight of testes, body and hind legs (for those that had hind legs), to the nearest 0.01 mg with a digital scale (Mettler AG245). We placed the left antenna and left front legs on a flat surface and photographed these dorsally in standardized positions under a dissecting microscope. We extracted ventral tubercles and photographed these anteriorly, to provide a clear measurement of the height of the major central tubercle from the abdomen. The seminal vesicles were removed and placed on a hemocytometer with a cover slip before being photographed. Seminal vesicle volume was calculated by multiplying depth of the hemocytometer by the seminal vesicle area measured from photographs. All photographs were taken under a Leica MZ75 dissecting microscope using a Leica DFC 290 camera, and measurements were taken using ImageJ 1.46r software (Abràmoff *et al.*, 2004). Sperm from seminal vesicles was diluted in insect ringer, smeared across a slide and photographed under a dark field using a Zeiss Axio-Imager compound microscope; the lengths of ten sperm were measured per individual, again using ImageJ.

In addition to experimental manipulation, we examined correlations between pre- and post-copulatory traits in a wild population to uncover the correlation among these traits in nature. We collected adult males from the wild and examined the correlations between weapons mass, body mass and testes mass. All measurements on wild males were taken with the same methodology as experimental individuals.

## Statistical analysis

We examined the effects of leg removal (hind or mid) on the size of eight morphological traits using separate general linear models with leg removal treatment as a categorical explanatory variable. Next, we constructed models to test for changes in the size of morphological traits relative to body mass. We built the initial models with body mass as a continuous covariate, treatment as a categorical factor, and the interaction between body mass and treatment. In all instances, we calculated

least-square means (adjusted means) from the general linear model for each treatment. Linear measurements such as antennae and front femur length were cube-transformed to convert their values to the same scale as mass for appropriate comparisons. All data were  $\log_{10}$ -transformed to improve linearity, normality and homoscedasticity. Our estimate of body mass was obtained by subtracting focal traits (testes mass and hind leg mass) from body mass to achieve an independent measure of body mass. This procedure helps to avoid the problem of part-whole correlations (Christians, 1999). All statistical analyses were conducted in R statistical software v0.99.893 (R Development Core Team, 2016). We collected 27 male insects from the wild and estimated the phenotypic scaling relationship between trait size and body size using OLS regression (Kilmer & Rodríguez, 2017).

## Results

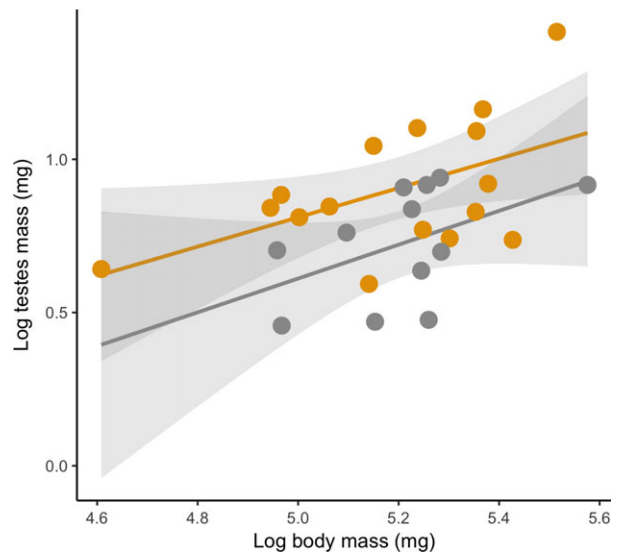
We initially examined the effects of leg removal (hind or mid) on the absolute size of eight morphological traits. Only testes mass was influenced by removal of the hind legs (Table 1, Figs 2 and 3). The remaining traits did not differ in size between hind leg and mid-leg removal treatments.

We next examined the scaling relationships between each of the traits and body mass using separate general linear models (GLMs). Our initial model included the main effects of body mass, leg removal treatment and interaction between body mass and treatment. Statistically significant interactions of body mass with treatment would indicate that the scaling slope of body mass and trait size changed depending upon whether the mid-legs or hind legs were removed. We did not find evidence of a change in scaling slope for any of the traits measured; thus, we removed the interaction and proceeded to test for a change in intercept due to treatment. We found evidence that males with their

**Table 1** Results of eight separate GLM for effects of leg removal on morphological traits in *Mictis profana* adults. Linear traits were cubed (except for sperm length), and all traits were log-transformed prior to analysis.

Trait measured	Wald chi-square	<i>P</i>
Testes mass	<b>5.183*</b>	<b>0.031*</b>
Abdominal tubercle length	0.551	0.466
Seminal vesicle volume	1.718	0.204
Sperm length	0.310	0.582
Body mass	0.055	0.815
Pronotum width	0.534	0.472
Antennal length	0.495	0.489
Front femur length	0.109	0.744

Error d.f. = 1 for all analyses; bold text indicates statistical significance. \*Indicates differences at  $P < 0.05$ .



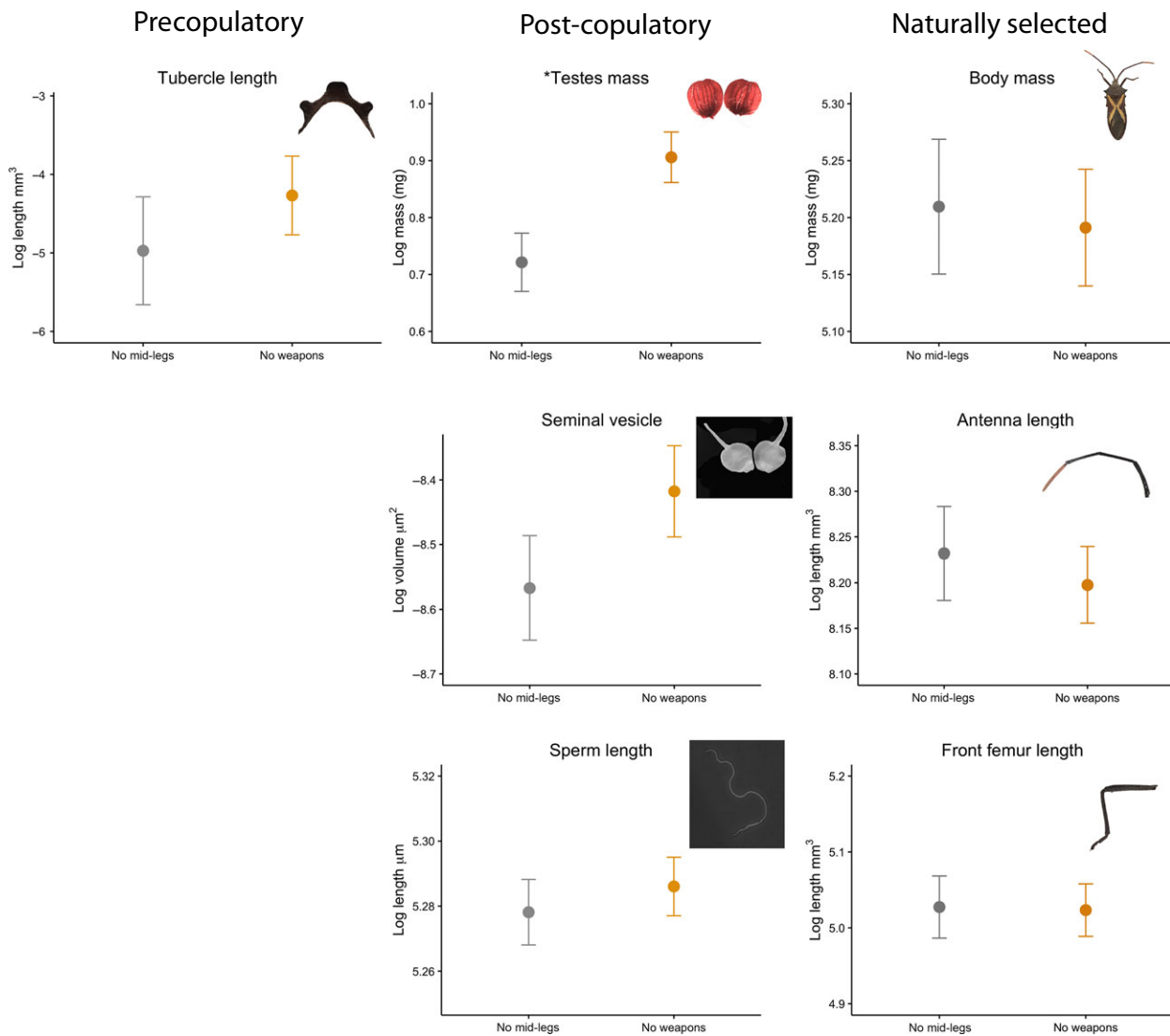
**Fig. 2** Testes size by treatment. Insects that developed without weapons (orange) invested disproportionately more in testes mass than insects that developed without mid-legs (grey). Testes weight increased with body weight, but treatment (hind legs removed) males developed proportionally heavier testes than did control males (mid-legs removed). Lines depict linear regression model predictions with 95% confidence interval bands.

hind legs removed grew disproportionately larger testes compared to other measured traits (Table 2, Figs 2 and 3). We did not find evidence that any other traits increased or decreased disproportionately relative to each other for males that lost their hind legs.

For wild-caught males, log testes mass and log body mass showed a positive relationship that did not differ significantly from isometry (linear regression against slope 1:  $F_{1,25} = 39.4$ ,  $P = 0.91$ ; OLS regression slope = 0.98, SE = 0.16,  $R^2 = 0.60$ : Fig. 4a). Further, the relationship between log weapon mass and log testes mass did not differ significantly from isometry (linear regression against slope 1:  $F_{1,25} = 30.1$ ,  $P = 0.17$ ; OLS regression: slope = 0.80, SE = 0.15,  $R^2 = 0.53$ : Fig. 4b).

## Discussion

We found, via an experimental manipulation, that weapons and testes experience a developmental trade-off in the coreid bug *M. profana*. Males that were prevented from investing in precopulatory weapons increased investment in testes mass. No increase in investment was found in any other structures measured in this study. Insects with their mid-legs removed did not differ in their relative allocation to testes mass. Although mid-legs accounted for a lower proportion of absolute mass than hind legs, males missing weapons allocated disproportionately more resources towards



**Fig. 3** Effect of weapon removal on precopulatory, post-copulatory and naturally selected traits. Graphs display body mass corrected investment in precopulatory, post-copulatory and naturally selected traits for treatments without hind legs (weapons) and without mid-legs. Least-squared means (adjusted means) were calculated using ANCOVA to account for differences in body mass for all traits (except for body mass itself). Testes mass was significantly larger in males without hind legs than males without mid-legs ( $P < 0.05$ ). Seminal vesicle volume showed a nonsignificant effect towards being larger in males without hind legs ( $P = 0.11$ ); \*Indicates significant differences among groups  $P < 0.05$  (photos by Ummat Somjee).

testes than males missing mid-legs. Insects that did not develop weaponry showed some evidence of growing significantly larger seminal vesicles (Fig. 3), a pattern that would be expected given that increased sperm production by larger testes may require seminal vesicles of greater volume for storage of sperm.

Insects in the family Coreidae express their weapons as a modification of hind legs that can be routinely ejected in response to various forms of entrapment (Embets *et al.*, 2016). For this reason, these insects provide an excellent opportunity for testing allocation trade-offs. Many studies on allocation trade-offs have

relied primarily on evidence of phenotypic correlations among pre- and post-copulatory traits. However, phenotypic correlations can offer little support for allocation trade-offs (Simmons *et al.*, 2017). Positive phenotypic correlations between traits are expected when individuals vary in resource acquisition and trait expression depends on resource availability (van Noordwijk & de Jong, 1986; de Jong & van Noordwijk, 1992; Reznick *et al.*, 2000).

Phenotypic correlations from wild populations may provide an important description of the natural phenotypic distribution of these traits in the wild; however,

**Table 2** Results of separate GLM for effects of leg removal on morphological traits in *Mictis profana* adult males with body mass as a covariate. Linear traits were cubed prior to direct comparison with body mass. All traits were log-transformed prior to analyses. Analyses were first run including main effects and the two-way interaction to test for differences in scaling slope due to treatment and between body mass and the trait in question. In all cases, the *P*-values for the interaction terms were not statistically significant and were removed, and the analyses were run with only main effects to test for a shift in the allometric intercept.

Trait measured	Body mass Wald chi-square	Treatment Wald chi-square
Testes mass	<b>8.619***</b>	<b>7.406**</b>
Abdominal tubercle length	4.087*	0.686
Seminal vesicle volume	0.496	1.917
Sperm length	0.273	0.342
Pronotum width	22.924***	0.287
Antennal length	2.271	0.267
Front femur length	9.079***	0.0056

Error d.f. = 1 for all analyses.

Bold text indicates traits that had a shift in their scaling relationship with body mass due to hind leg removal.

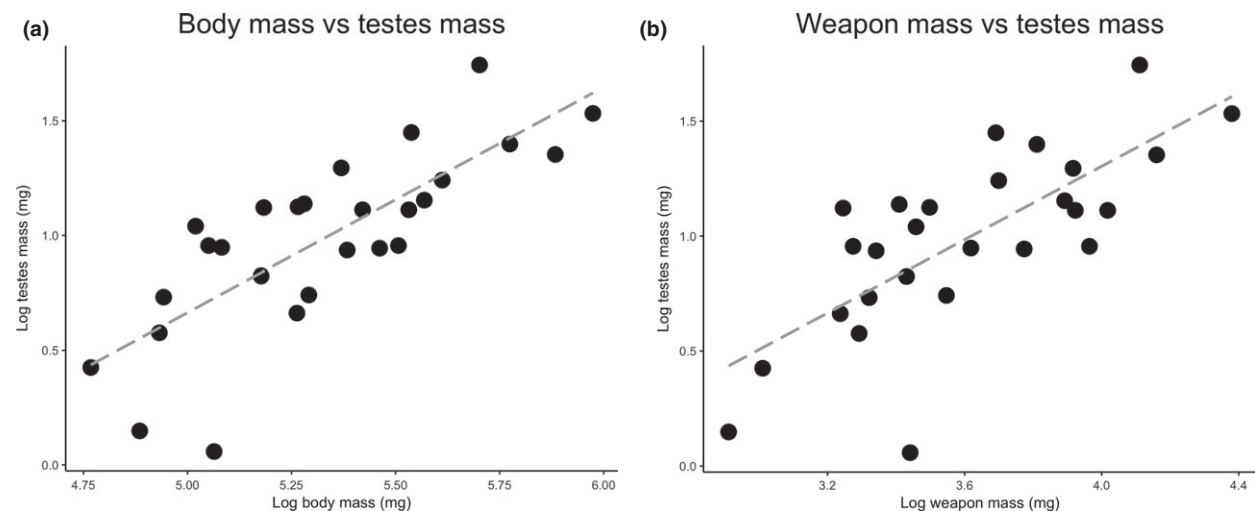
\* $P < 0.05$ , \*\* $P < 0.01$ , \*\*\* $P < 0.001$ .

these data do not provide information on within-organism resource allocation trade-offs (Simmons *et al.*, 2017). Allocation trade-offs can be obscured by environmental effects, and experimental manipulations that hold all other variables constant are necessary to reveal allocation trade-offs among pre- and post-copulatory sexual traits (Simmons & Emlen, 2006). Indeed, we found a positive correlation between weapons and testes in our field-collected individuals (Fig. 4), whereas

the development of weapons had a negative impact on testes in our experimental manipulation. Similar patterns have been found in stalk-eyed flies, wherein eye span and testes size are positively correlated among individuals (Rogers *et al.*, 2008; Cotton *et al.*, 2010) yet experimental manipulations provide direct evidence of a trade-off between these traits (Fry, 2006).

Environmental conditions during development can also alter the relative expression of both weapons and testes. In a related Coreid species, the heliconia bug, males reared on one host plant produced larger testes but smaller weapons compared to males reared on a separate host plant (Somjee *et al.*, 2015). This environmentally induced change in relative testes size was of moderate but significant effect (Cohen's  $d = 0.70$ , Somjee *et al.*, 2015). In another study, removal of a single hind leg of leaf-footed cactus bugs during their fourth instar resulted in adults with proportionally larger testes compared to a group where a single mid-leg was removed (Cohen's  $d = 0.39$ , Joseph *et al.*, 2017). In comparison, in our study, males that were prevented from developing both hind legs had an increase in testes size approximately one standard deviation larger than insects that developed without mid-legs (Cohen's  $d = 1.01$ ). In our study species, weapons are much larger than mid-legs and we could not determine whether preventing development of weapons had a proportionally larger effect on testes development per gram of tissue compared to mid-legs. The cost of producing weapons, relative to other somatic tissues, remains a major question in studies that examine allocation trade-offs in sexually selected traits (Simmons *et al.*, 2017).

In many systems, it is difficult to distinguish whether correlated traits are more strongly influenced by a shared



**Fig. 4** Testes size in wild-caught males. In wild-caught males, both testes mass (OLS regression: slope = 0.98, SE = 0.16,  $R^2 = 0.60$ ) and weapon mass (slope = 0.80, SE = 0.15,  $R^2 = 0.53$ ) have relationships not significantly different from isometry (linear regression against slope 1: body mass:  $F_{1,25} = 39.4$ ,  $P = 0.91$ ; weapon mass:  $F_{1,25} = 30.1$ ,  $P = 0.17$ ). These positive correlations in wild males do not provide any indication that an allocation trade-off is underlying the development of pre- and post-copulatory traits in this insect.

developmental structure (Klingenberg 2005) or by correlated selection (Cheverud, 1996). By manipulating the development of a single precopulatory weapon, here we decouple this relationship and expose a resource allocation trade-off among what appear to be developmentally distinct traits. Our finding that investment in male hind legs trades off with investment in testes and not with development of another close-by putative precopulatory structure (tubercles) supports the idea that testes and weapons are developmentally integrated through a history of correlated selection (Simmons & Emlen, 2006). To date, few studies have experimentally investigated resource allocation trade-offs among pre- and post-copulatory traits (Simmons *et al.*, 2017). In one well-studied case, onthophagine dung beetles, males experimentally prevented from growing horns had increased relative investment in testicular tissue (Simmons & Emlen, 2006), whereas males prevented from developing primary genitalia increased their allocation to horn growth (Moczek & Nijhout, 2004). In our study, the behavioural feature of weapon autotomy (Embets *et al.*, 2017) provided an opportunity to prevent weapon development with minimal potential injury and detrimental effects to developing insects and resulted in increased allocation of resources to testes growth.

Our investigation of a hemimetabolous insect provides additional insights into the developmental links between exaggerated trait growth and allocation trade-offs. Previous studies have experimentally halted trait growth in holometabolous insects such as dung beetles and stalk-eyed flies. In closed developmental systems such as those of holometabolous insects, animals undergo a single, relatively rapid transition between larval and adult forms, and feeding does not occur during this closed transitional pupal stage. Where a developing organism must allocate a limited set of resources to multiple rapidly developing traits, the potential for trade-offs is high. However, resource allocation trade-offs are thought less likely in open developmental systems such as those of hemimetabolous insects (e.g. Tomkins *et al.*, 2005) because growth occurs in a step-wise fashion, with each successive instar able to feed as it develops towards adulthood. Here, we prevented trait growth in such a system, where males could feed to compensate for resources lost in a previous instar and potentially invest equally in all traits and yet we found evidence of a trade-off between weapons and testes. There are a number of reasons that may explain this observed resource allocation trade-off. The proportional investment in hind legs increases significantly during the final moult to adulthood, and there might be a limit to which insects can compensate for lost resources and distribute these resources equally to all traits before they moult. In our sample, the hind legs of fifth-instar male *M. profana* nymphs comprised on average 10.4% of total somatic tissue. As nymphs moult from 5th instar into adulthood, the proportional investment in

hind leg mass thus increases by up to 47.1%. This large increase in relative allocation to hind legs during the final moult may provide an opportunity for disproportionate allocation among traits, despite the open developmental system. Hemimetabolous insects will be useful to test theoretical predictions about how distinct developmental processes might limit or enhance the potential for selection to drive trade-offs among traits when resource availability differs (Toubiana & Khila, 2016). Future studies might examine the ontogeny of such trade-offs by examining resource allocation decisions at different discrete stages of development.

Among Coreid species, large body and weapon size in males contribute to success in territory defence against rival males (Miyatake, 2002) and success in premating combat (Mitchell, 1980). There is also evidence that testis size contributes to post-mating reproductive success. In an experimental manipulation similar to ours, Joseph *et al.* (2017) found that males who developed without a single hind leg also developed larger testes and that females mated to these males who laid viable eggs had a higher proportion of live hatchlings (Joseph *et al.*, 2017), suggesting a role of testes size in reproductive success. Although we found no difference in sperm length between our treatments, it is possible that other ejaculate traits such as sperm number, motility and seminal fluid composition might also be affected, which are likely to contribute to post-copulatory competitive fertilization success (Parker, 1998; Simmons & Kotiaho, 2002; Snook, 2005). Our study contributes to a small but growing body of work that supports the prediction that males should face a trade-off between expenditure on gaining mates and on gaining fertilizations (Parker *et al.*, 2013; Simmons *et al.*, 2017). Moreover, our findings illustrate the importance of experimental manipulation for detecting the presence of life-history trade-offs more generally (Ketterson & Nolan, 1992).

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## Authors' contributions

US, LWS, CWM and NT conceived the ideas and designed methodology; US, NT and LWS collected the insects, and US performed dissections and measurements; US and CWM analysed the data; US led the writing of the manuscript. No authors in this manuscript have conflict of interest to declare. All authors contributed critically to drafts and gave final approval for publication.

## Data accessibility

All data will be deposited in the Dryad repository upon acceptance.

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