



Do males that experience weapon damage have greater reproductive potential than intact males in polygynous scenarios?

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Abstract

Males with damaged weapons often lose intraspecific contests; however, recent research suggests these males may use post-copulatory means to mitigate reduced reproduction. When intraspecific competition is absent, can weapon-damaged males produce more offspring in multi-mating scenarios relative to intact males? We examined the reproductive potential of weapon-damaged males in *Narnia femorata* (Hemiptera: Coreidae), a species that exhibits resource defense polygyny and is known to increase testes size when developmental weapon damage occurs. We induced weapon damage during development. Upon sexual maturation, we provided intact and weapon-damaged males with access to four unmated females successively and without any competitors. The mating partners of weapon-damaged males were more likely to have their eggs hatch. Furthermore, weapon-damaged males produced more offspring, though only with larger females. These results suggest that weapon-damaged males have enhanced fertilization outcomes, potentially minimizing reproductive costs of weapon damage.

Significance statement

Weapon damage is common in nature and can reduce pre-copulatory success. However, few studies have examined the reproductive consequences of weapon damage. We tested the hypothesis that weapon-damaged males can compensate for a pre-copulatory disadvantage through increased investment in traits that improve post-copulatory fertilization success. To examine the reproductive potential of weapon-damaged males, we provided males with four females in succession, then measured reproductive outcomes. We found that mating partners of weapon-damaged males were more likely to have their eggs hatch relative to the mating partners of intact males. Furthermore, we found that weapon-damaged males produced a larger number of offspring than intact males. This evidence reveals that weapon damage allows males to boost reproductive outcomes in non-competitive contexts.

Keywords Autotomy · Multiple mates · Trade-off · Sexual selection · Alternative reproductive tactic · Conditional strategy

Introduction

Animals have evolved a multitude of elaborate weapons that they use in intraspecific competition (Emlen 2008). Individual

differences in weapons can be a strong determinant of success in these contests (Clutton-Brock 1982; Sneddon et al. 1997; Karino et al. 2005; Emlen 2008; Small et al. 2009; Suzaki et al. 2015) and differences can arise due to damage. Weapon damage is common in nature (Mattlin 1978; Berzins and Caldwell 1983; Umbers et al. 2012; Jennings et al. 2017; Lane and Briffa 2017; Wong et al. 2018), e.g., reaching 30% in white-tailed deer (Karns and Ditchkoff 2012) and 82% in tule elk (Johnson et al. 2005). Weapons can be damaged through intraspecific fights (Mattlin 1978; Clutton-Brock 1982; Siva-Jothy 1987; Jennings et al. 2017), predator interactions (Hoadley 1937), disease (Adamo et al. 1995), or developmental irregularities (Embets et al. 2016).

Males with damaged weapons typically lose pre-copulatory competitions (Mattlin 1978; O'Neill and Cobb

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1979; Berzins and Caldwell 1983; Yasuda et al. 2011; Emberts et al. 2018), which can be a detriment to reproductive success (Wong and Candolin 2005; Emberts et al. 2018). However, males may be able to change resource allocation and investment decisions to make the best of this bad situation (Simmons et al. 2017). The loss of a pre-copulatory weapon during development may cause males to redirect investment towards enhancing post-copulatory reproductive traits (Simmons and Emlen 2006; Somjee et al. 2017; Joseph et al. 2018), leading to greater female fertilizations. Reproductive trade-offs between pre- and post-copulatory traits due to a fixed energy budget are a fundamental assumption made in sperm competition theory (Birkhead and Møller 1998, Parker and Pizzari 2010). Research supports a weapons-testes trade-off (Evans and Garcia-Gonzalez 2016, Simmons et al. 2017) including studies that manipulated weapons which enhanced post-copulatory traits in dung beetles (Simmons and Emlen 2006) and stalk-eyed flies (Fry 2006). However, these manipulations were manufactured in the laboratory and were not a result of trauma that an animal would encounter in the wild. Thus, we have limited knowledge in understanding how natural weapon damage would affect post-copulatory traits (Somjee et al. 2018; Joseph et al. 2018; Miller et al. 2019; Cavender et al. 2021) and fertilization outcomes (Joseph et al. 2018). Since polygynous mating systems that promote sperm competition are incredibly common in the animal kingdom, understanding how weapon damage affects patterns of offspring production under multi-mating scenarios is crucial to understanding the extent to which post-copulatory investments may help males compensate for a pre-copulatory disadvantage.

Narnia femorata, the leaf-footed cactus bug, has a resource defense polygyny mating system. Males engage in intraspecific competition using their enlarged hind leg weapons to stomp, kick, or squeeze other males to gain access to territory that attracts females (Proctor et al. 2012; Nolen et al. 2017). Males of this species can undergo autotomy (i.e., limb loss, Fig. 1) if a hind leg gets entrapped in a molt or caught by a predator (Emberts et al. 2016). Males use both hind legs as the

weapon to fight their opponent in contests (Proctor et al. 2012) and are five times less likely to win competitions if they have a damaged weapon that is only comprised of a single hind leg (Emberts et al. 2018). Single-leg autotomy is common in the wild (i.e., 12%) (Emberts et al. 2016). Interestingly, testes grow 15–39% larger by adulthood if one hind leg is autotomized during development (Joseph et al. 2018; Miller et al. 2019), which may be due to their increased sperm production (Cavender et al. 2021). The larger size and increased sperm production of the testes suggest that autotomized males may be capable of enhanced fertilization capacity, at least in contexts without pre-copulatory competition. Wild population density of *N. femorata* can fluctuate across space and time, providing opportunities for males to encounter females without rivals present (Cirino and Miller 2017). Furthermore, there is no evidence of a difference in female receptivity to intact and weapon-damaged males (Emberts et al. 2018, Fig. 1). This species thus provides an opportunity to study the reproductive potential of males with damaged weapons.

The reproductive potential of weapon-damaged and intact males was examined under monogamous and non-competitive conditions in Joseph et al. (2018). This study showed that *N. femorata* females that mated with weapon-damaged males compared to intact males (1) had no differences in egg laying probability, (2) had a lower likelihood of their eggs hatching, and (3) in cases where females produced viable offspring, females produced greater numbers of offspring (Joseph et al. 2018). Our objective here was to investigate whether the post-copulatory reproductive advantage for weapon-damaged males found in the Joseph et al. (2018) study would persist under multi-mating conditions which might reveal a more complete picture of male reproductive potential.

Here, we tested the hypothesis that weapon-damaged males compensate for a pre-copulatory disadvantage through increased post-copulatory fertilization success under multi-mating conditions. We predicted that, in a non-competitive setting, and compared to males with intact weapons, weapon-damaged males will have either (i) greater per mating

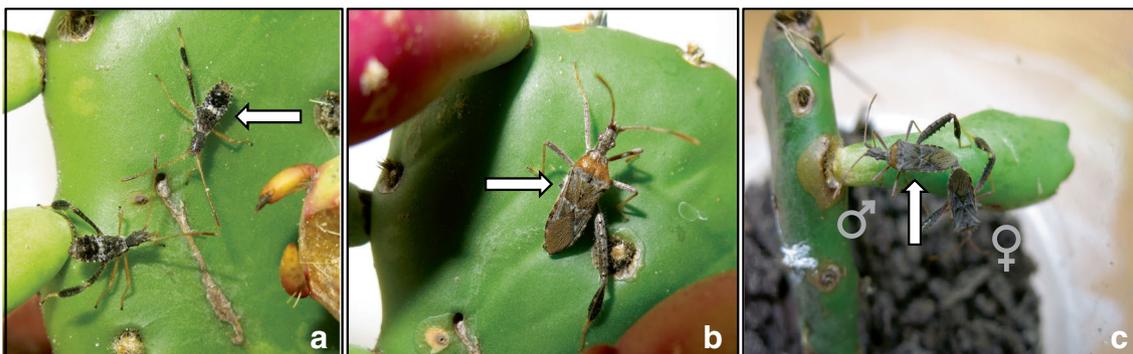


Fig. 1 Juvenile and adult *Narnia femorata* with damaged weapons. Intact (left) and weapon-damaged (right) juveniles (a). Adult weapon-damaged male (b). Weapon-damaged male mating with a female (c). White arrows denote the missing hind limbs that produced incomplete weapons

fertilization success; and/or (ii) sustain higher fertilization success over all sequential copulation opportunities. We induced males to drop a single hind limb during juvenile development (Fig. 1), resulting in an incomplete or damaged weapon, much like an elk with a missing antler. After damage occurred and upon sexual maturity, we examined adult fertilization outcomes. We provided males with four unmated females consecutively for 24 h per female. The purpose of providing one female after another was to challenge sperm reserves. Then, we measured male reproductive potential by quantifying eggs and offspring. We predicted that females later in the mating order would produce fewer offspring due to sperm depletion.

Methods

Insect rearing

Adult *N. femorata* and cacti (*Opuntia mesacantha* ssp. *lata*) were collected in North Central Florida in 2018 (July–September). These adults were paired and potted in a deli cup with a fruited cactus pad. Pairs were left to mate and lay eggs freely. Offspring from these 21 mating pairs were used in the experiments.

Eggs were separated from parental pairs, but kept in identical nutritional conditions, and placed in either incubators (Percival Scientific I-30VL) or a temperature-controlled rearing room (26 °C, 14:10 light/dark) to hatch. We raised 1st–3rd instars in groups (5–12) based on their natural aggregation propensity (Cirino and Miller 2017) and because an increase in survivorship comes with group rearing (Allen and Miller 2020). Cups were checked daily for cactus quality and insect maturation. Fourth instars were randomly selected from both rearing locations for treatment, separated into their own deli cup, and placed in a greenhouse (21–32 °C, 14:10 L/D) to develop into sexually mature adults. Diet can affect the body and gonad condition in *N. femorata* (Sasson et al. 2016; Cirino 2020), so every individual was provided a newly harvested cactus pad with fruit to ensure access to high-quality food. Fourth instars were chosen for treatment (Fig. 1) because heteropterans experience the largest gonad development beginning at this stage (Economopoulos and Gordon 1971; Dumser and Davey 1974) and to resemble a previous protocol (Joseph et al. 2018; Miller et al. 2019).

Treatments

Every insect was randomly assigned to either the weapon-damaged or intact treatment. We followed the single-leg autotomy protocol established in previous experiments for treatment (Video S1) (Joseph et al. 2018; Miller et al. 2019). Insects of this species cannot regenerate entire limbs (Embets et al. 2016; Embets et al. 2017). Thus, loss of a hind

limb causes permanent weapon damage (Fig. 1). Sex is difficult to determine before adult eclosion so both males and females, damaged and intact, were produced. All males and only the intact females were used in the subsequent experiments. This is a change from Joseph et al. (2018) where both damaged and intact females were used to test effects of autotomy on offspring production. Individuals originating from across the range of juvenile group sizes were represented in each treatment.

Mating protocol and reproductive potential

Males that were at least 28 days post-adult eclosion ($n = 38$) were assigned 4 different non-sibling, unmated females ($n = 152$) for mating. One female was provided per day over 4 consecutive days. All females were at least 14 days post-adult eclosion (i.e., sexually mature) (Cirino 2020). Mating pairs were maintained in a rearing room (26 °C, 14:10 L/D). Males were sequentially paired with each assigned female partner for 24 h and allowed to mate freely (time protocol established in Joseph et al. 2018). Since males have reduced sperm numbers directly after being paired with a female (Greenway et al. 2020), males were deemed unlikely to replenish sperm reserves within 24 h. After the end of the 4-day period, males were removed from the last female partner's cup and immediately euthanized. Females were kept in their individual containers to lay eggs for 2 weeks. This represents an estimated 67% of their reproductive lifespan in wild North Central Florida populations (Cirino and Miller 2017; Cirino 2020). Females were then euthanized and their eggs were left to hatch for another 2 weeks, which is a sufficient time for fertilized eggs to hatch in this species (Vessels et al. 2013). The numbers of eggs laid and hatched were then quantified. Since the eggs were kept in containers labeled only by female ID, observers were blind to all factors of interest (e.g., damage treatment, mate order) until after egg data was collected.

Photographing and measurements

Body size is known to be tied to the number of eggs females can produce in *N. femorata* (Miller et al. 2013) and other insects (Honěk 1993; Bonduriansky 2001). Egg and offspring production can vary widely in *N. femorata* ranging from 0 to 278 eggs laid in a month with up to 91% of those eggs hatching (Wilner et al. 2020). Therefore, we measured females, then used a composite metric of female body size as a covariate in analyses (see below). Male body size was also considered because female *N. femorata* mate more readily with larger males (Gillespie et al. 2014). Since male body size and testes size are highly correlated (Greenway et al. 2020), larger males may produce more sperm and fertilize more eggs (e.g., Kant et al. 2012a).

Table 1 Analysis of the components of male reproductive success. Results from three separate generalized linear mixed models (GLMMs) that address the components of offspring production leading to increased fertilization success. Bolded terms indicate statistical significance ($p < 0.05$)

Source	Eggs laid (Y/N)		Eggs hatched (Y/N)		Offspring number (count)	
	Wald χ^2	<i>p</i> value	Wald χ^2	<i>p</i> value	Wald χ^2	<i>p</i> value
Weapon damage	1.910	0.167	5.164	0.023	1.928	0.165
Mate order	2.708	0.100	1.385	0.239	0.830	0.362
♀ (PC1)	13.026	≤ 0.001	1.020	0.313	7.164	0.007
♂ (PC1)	2.164	0.141	1.878	0.171	1.835	0.176
Weapon damage × ♀ (PC1)	N/A	N/A	N/A	N/A	25.359	≤ 0.001
Mate order × ♀ (PC1)	N/A	N/A	N/A	N/A	2.791	0.095
Mate order × ♂ (PC1)	N/A	N/A	N/A	N/A	2.830	0.093

All df = 1

We photographed all euthanized adults using a digital camera (Canon EOS 50D, Canon, Tokyo, Japan). These images were used to procure six linear body size measurements (Supplementary Material S1) using ImageJ software (v1.42d) (Abràmoff et al. 2004). These measurements were used in the principal component analyses (PCAs) described below.

Statistical analysis

We loaded six linear body size measurements into a PCA. We ran one for each sex separately. We used a correlation matrix to reduce our body size measurements into one composite measure per sex (Supplementary Material S1-3). We then ran a regression of PC1 values versus pronotum width (PW) measurements, which is commonly used as a proxy for body size in hemipterans. We found that these values are highly correlated (Supplementary Material S4). Additionally, we found only one significant principal component (PC1) per sex, which explained 92% of the variation in morphological data for males and 89% for females (Supplementary Material S1-4); therefore, we used PC1 scores for both male and female body size in the following analyses.

To investigate factors that may contribute to offspring production, we examined our data using three separate generalized

linear mixed models (GLMMs) using the *lme4* package in R (R Core Team 2021). For all three models, male weapon damage (Y/N) and mate order (1, 2, 3, 4) were included as the explanatory variables. Female PC1 and male PC1 were used as covariates and male ID was included as a random effect. Our first two models used GLMMs assuming a binomial distribution (logit link) and either egg production (Y/N) or hatching success (Y/N) as the response variable. In our third GLMM, we assumed a Poisson distribution (log link) with the number of offspring as the response variable. We used AIC model selection to compare multiple GLMM models that included all main effects described above and all two-way interactions between them (AICtab in *bbmle* package). The most parsimonious model was identified by the lowest AIC score (Supplementary Material S5) and reported in the “Results” section. All analyses in this manuscript were performed in R v 4.0.4 (R Core Team 2021).

Results

Larger females were more likely to lay eggs (binary: yes/no) during our study period (Table 1). We found that male weapon damage did not affect the likelihood of female egg laying (Table 1, Fig. 2). However, females were more likely to have

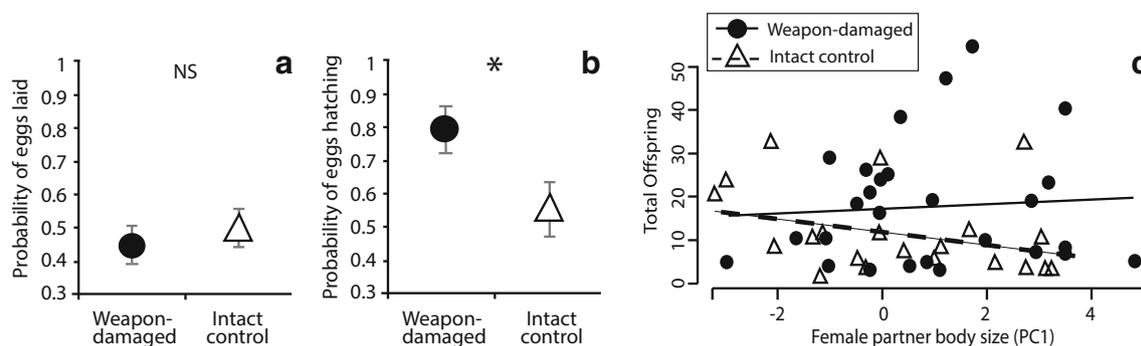


Fig. 2 Weapon damage does not affect the likelihood of egg laying (NS = not significant) (a); however, weapon-damaged males are more likely to have hatched eggs (\pm SE) (the asterisk indicates significant result) (b). If

eggs did hatch, weapon-damaged males (solid line) produced more offspring when mated with large females compared to intact males (dashed line) (c)

at least one egg hatch (binary: yes/no) when they mated with weapon-damaged males (Table 1, Fig. 2). Twenty-seven of the 34 females (79.4%) that mated with weapon-damaged males and 21 of the 38 females (55.3%) that mated with intact males had at least some hatching success. Of those females, 55.6% (15/27) that mated with weapon-damaged males and 28.6% (6/21) that mated with intact males had all eggs hatch. Finally, we found that weapon-damaged males produced more offspring than intact males but only when paired with larger females (Table 1, Fig. 2, autotomy slope = 0.098, $p = 0.015$; intact slope = -0.208 , $p < 0.001$). This difference appears to be driven by the decline in offspring number of intact males mated with large females compared with small females. Surprisingly, mate order did not affect fertilization success across the four females provided to males (Table 1).

Discussion

Hunters and naturalists alike know the ubiquity of damage to sexually selected horns and antlers of bovids. While weapon damage is pervasive among many animal taxa in the wild, our knowledge is limited with regard to the reproductive consequences of this damage (Simmons and Emlen 2006, Johnson et al. 2007, Jennings et al. 2017, Joseph et al. 2018, Somjee et al. 2018, Cavender et al. 2021). Few studies have examined the effect of weapon damage on post-copulatory traits (Simmons and Emlen 2006, Joseph et al. 2018, Somjee et al. 2018), and only one experimental study has investigated how weapon damage affects reproductive success (Joseph et al. 2018). In this study, we focused on the reproductive potential of male insects that experienced developmental weapon damage. We know from previous work that weapon-damaged males in *N. femorata* have larger testes (Joseph et al. 2018; Miller et al. 2019), which produce more sperm (Cavender et al. 2021). Furthermore, testes size is correlated with reproductive success (Greenway et al. 2020). Here, we experimentally manipulated weapon damage and examined the reproductive potential of these males by providing multiple mates in the absence of male-male competition. The female partners of weapon-damaged males were more likely to have eggs hatch. When paired with larger females, weapon-damaged males produced more offspring than intact males. This difference in offspring number was driven primarily by the decline of offspring production of intact males mated with large females compared to small females, a curious result that warrants further investigation in the future. Nevertheless, large invertebrate females are known to produce more eggs than smaller females (Honěk 1993; Bonduriansky 2001; Miller et al. 2013) and *N. femorata* is no exception (Miller et al. 2013). Thus, high fecundity females may benefit from mating with weapon-damaged males.

Females that mated with weapon-damaged males had a higher probability of hatching success than females that mated with intact males. While increased sperm numbers could account for greater offspring number, sperm number alone would not explain the increased likelihood of hatching success. It is possible that seminal fluid proteins (SFPs) also change in weapon-damaged males. SFPs, produced in the accessory glands, mix with sperm to form the ejaculate. These SFPs can promote sperm storage, maintenance, and release from the spermatheca in the female (Avila et al. 2011), which may promote fertilization success. In *Drosophila melanogaster*, sperm storage and utilization depend on SFPs that, when absent, do not allow for sperm to fertilize eggs; therefore, females lay infertile eggs (Xue and Noll 2000). If SFPs deplete across multiple mates even if sperm does not, fertilization may not occur. Like testes (Greenway et al. 2020), accessory glands are metabolically expensive (Benoit et al. 2020). Thus, when resources are freed up through damage to a metabolically expensive weapon, as done in this experiment, accessory glands that produce more SFPs may also grow larger. An increase in SFPs, in addition to an increase in sperm number (Cavender et al. 2021), for weapon-damaged males may play an integral role in the increased fertilization success that we observed here, though no study has examined SFPs in *N. femorata* yet.

Weapons that are used for intraspecific competition are frequently damaged in *N. femorata* (Emberts et al. 2016). Increasing investment in testes (Joseph et al. 2018, Miller et al. 2019) and ejaculates might be a means by which *N. femorata* males can partially compensate for damaged weapons. Although weapon-damaged males may be able to achieve some mating success, this success appears to be reduced for these males when intact males are present (Emberts et al. 2018). In the current study, we found that large females were more likely to lay eggs than smaller females; however, this was not detected in the Joseph et al. (2018) study. When mating with a single partner, Joseph et al. (2018) found that females who were paired with weapon-damaged males were less likely to produce eggs that hatched, whereas, in the present study using multi-mating conditions, we found the opposite result. However, under both single (Joseph et al. 2018) and multi-mating conditions (current study), similar results regarding offspring production were found. When females produced viable offspring, females that mated with weapon-damaged males produced more offspring than those females that mated with intact males, though in the present study this only occurred with large females. It is intriguing that the results are somewhat different, though there are a few methodological differences between the two studies. First, the experiments were completed at different times of the year: mid-breeding season (Joseph et al. 2018) and late in the breeding season (current study). *N. femorata* overwinters (i.e., quiescence) and shuts down reproductive activity at the end of the

breeding season (Cirino 2020). Some of the insects in the present study may have entered this phase during our experiment affecting our results (Cirino 2020). Second, the variation in female body size was greater in our study (2.66–5.30 mm) compared to the Joseph et al. (2018) study (3.12–5.18 mm). The larger variation in body size in our study may have enabled us to detect the association between female body size and offspring number between the two groups of males. Finally, the hind-limb status of female partners, autotomized or intact, also differed between studies. In the Joseph et al. (2018) study, males were provided with female partners that either had autotomized or intact hind limbs; whereas, in the present study, males were only provided with intact females. Loss of a hind limb in females has been associated with an increase in ovary mass (Miller et al. 2019). Thus, this difference in protocol may have contributed to the differences in our results. Regardless, the overall message of the current study supports the findings of Joseph et al. (2018) and further shows that males have greater reproductive potential than intact males when they have access to multiple large female partners. Our study contributes to the small but growing body of literature that suggests reproductive trade-offs occur between weapons and testes. Understanding the reproductive outcomes in a polygynous mating system is an important step in understanding the implications of weapon damage on male fitness, a situation common to many animals in the wild.

We examined the offspring production of four females presented to males in a sequence, and we predicted that the latter females would have decreased offspring production due to the effects of sperm depletion. This was not the case. Many other species across taxa (Nakatsuru and Kramer 1982; Rubolini et al. 2007; Hetttyey et al. 2009; Weir and Grant 2010; Swierk et al. 2015) and within Insecta (King 2000; Jones 2001; Elzinga et al. 2011; Kant et al. 2012b; Makatiani et al. 2013; Michaud et al. 2013) are known to deplete sperm across multiple mates. Regardless of mate order and treatment, about half of the females in this experiment did not produce any eggs. This number was a surprise to us since *N. femorata* can lay unfertilized eggs. We ran our experiment when insects were producing the final generation of the breeding season, and some females may have already begun quiescence (Cirino 2020). Thus, females may have been reluctant to mate during the time that they spent with their mating partner, which may have allowed males time to replenish their sperm reserves.

Males live in a socially dynamic world and the presence of another male will often change reproductive outcomes (Andersson 1994). We expect the results documented here to be a “best case” scenario for weapon-damaged males because they did not have to overcome another male to access a female. Experimental research on the consequences of weapon damage under competitive scenarios is scarce but shows that intact males have an advantage over weapon-damaged males in physical contests before mating (Berzins and

Caldwell 1983; Emberts et al. 2018). However, in complex ecological scenarios, some weapon-damaged males can access females, though mating success can be reduced compared to intact males (Emberts et al. 2018). Depending on factors such as population and resource density, weapon-damaged males may only obtain a few copulations in their lifetime. Our simplification of the complexities of the natural world has demonstrated that weapon-damaged males have higher reproductive potential. One next step is to investigate the reproductive consequences of weapon damage under alternative scenarios where the behavior and fertilization success of multiple males and females can be tracked.

Weapon quality is not always easily visible to human observers. Like other animal tissues, the weapons of sexual selection can be compromised in many ways. For example, they may grow large, but lack strength, they may be compromised by disease, or they may accumulate stress fractures from combat. Weapon damage may be common, but the consequences of weapon damage are wildly understudied (Simmons and Emlen 2006, Johnson et al. 2007, Jennings et al. 2017, Joseph et al. 2018, Somjee et al. 2018, Cavender et al. 2021) and more work should continue to explore this phenomenon. Assessing the consequences of weapon damage is an intriguing path for future research, potentially informing our understanding of animal behaviors and life history more generally.

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s00265-021-03019-y>.

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Author contribution LAC and CWM conceived, designed, and analyzed the data for the study. LAC and SHL performed the experiment and collected the data. All three authors wrote the manuscript.

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Data availability Our data file used for analyses is included as an electronic file in the Supplementary Material.

Code availability R code is included as an electronic file in the Supplementary Material.

Declarations

Ethics approval Not applicable

Consent to participate Not applicable

Consent for publication All persons that are entitled to authorship have been included as authors and all authors have read and consented to the manuscript submitted.

Conflict of interest The authors declare no competing interests.

References

- Abràmoff MD, Magalhães PJ, Ram SJ (2004) Image processing with ImageJ. *Biophoton Int* 11:36–42
- Adamo SA, Robert D, Hoy RR (1995) Effects of a tachinid parasitoid, *Ormia ochracea*, on the behavior and reproduction of its male and female field cricket hosts (*Gryllus spp.*). *J Insect Physiol* 41:269–277
- Allen P, Miller CW (2020) The hidden cost of group living for aggregating juveniles in a sexually dimorphic species. *Biol J Linn Soc* 131:39–49
- Andersson MB (1994) Sexual selection. Princeton University Press, Princeton, NJ
- Avila FW, Sirot LK, LaFlamme BA, Rubinstein CD, Wolfner MF (2011) Insect seminal fluid proteins: identification and function. *Annu Rev Entomol* 56:21–40
- Benoit JB, Bose J, Bailey ST, Polak M (2020) Interactions with ectoparasitic mites induce host metabolic and immune responses in flies at the expense of reproduction-associated factors. *Parasitol* 147:1196–1205
- Berzins IK, Caldwell RL (1983) The effect of injury on the agnostic behavior of the stomatopod, *Gonodactylus bredini* (Manning). *Mar Behav Physiol* 10:83–96
- Birkhead TR, Møller AP (1998) Sperm competition and sexual selection. Academic Press, London, UK
- Bonduriansky R (2001) The evolution of male mate choice in insects: a synthesis of ideas and evidence. *Biol Rev* 76:305–339
- Cavender K, Ricker T, Lyon M, Shelby E, Miller CW, Moore PJ (2021) The trade-off between investment in weapons and fertility is mediated through spermatogenesis in the leaf-footed cactus bug *Narnia femorata*. Authorea. <https://doi.org/10.22541/au.161046099.92330872/v1>
- Cirino LA (2020) Consequences of environmental heterogeneity on reproductive output in the leaf-footed cactus bug *Narnia femorata* (Hemiptera: Coreidae). University of Florida, Doctoral dissertation
- Cirino LA, Miller CW (2017) Seasonal effects on the population, morphology and reproductive behavior of *Narnia femorata* (Hemiptera: Coreidae). *Insects* 8
- Clutton-Brock TH (1982) The functions of antlers. *Behaviour* 79(2–4):108–124
- Dumser JB, Davey KG (1974) Endocrinological and other factors influencing testis development in *Rhodnius prolixus*. *Can J Zool* 52:1011–1022
- Economopoulos AP, Gordon HT (1971) Growth and differentiation of testes in large milkweed bug, *Oncopeltus fasciatus* (Dallas). *J Exp Zool* 177:391–405
- Elzinga JA, Chevasco V, Grapputo A, Mappes J (2011) Influence of male mating history on female reproductive success among monandrous Naryciinae (Lepidoptera: Psychidae). *Ecol Entomol* 36:170–180
- Emberts Z, Miller CW, Kiehl D, St Mary CM (2017) Cut your losses: self-amputation of injured limbs increases survival. *Behav Ecol* 28:1047–1054
- Emberts Z, St Mary C, Miller C (2016) Coreidae (Insecta: Hemiptera) limb loss and autotomy. *Ann Entomol Soc Am* 109:678–683
- Emberts Z, St Mary CM, Herrington TJ, Miller CW (2018) Males missing their sexually selected weapon have decreased fighting ability and mating success in a competitive environment. *Behav Ecol Sociobiol* 72:81
- Emlen D (2008) The evolution of animal weapons. *Annu Rev Ecol Evol Syst* 39:387–413
- Evans JP, Garcia-Gonzalez F (2016) The total opportunity for sexual selection and the integration of pre- and post-mating episodes of sexual selection in a complex world. *J Evol Biol* 29:2338–2361
- Fry CL (2006) Juvenile hormone mediates a trade-off between primary and secondary sexual traits in stalk-eyed flies. *Evol Dev* 8:191–201
- Gillespie SR, Tudor MS, Moore AJ, Miller CW (2014) Sexual selection is influenced by both developmental and adult environments. *Evolution* 68:3421–3432
- Greenway EG, Cirino LA, Wilner D, Somjee U, Anagnostou ME, Hepple RT, Miller CW (2020) Extreme variation in testes size in an insect is linked to recent mating activity. *J Evol Biol* 33:142–150
- Hettyey A, Vagi B, Hevizi G, Torok J (2009) Changes in sperm stores, ejaculate size, fertilization success, and sexual motivation over repeated matings in the common toad, *Bufo bufo* (Anura: Bufonidae). *Biol J Linn Soc* 96:361–371
- Hoadley L (1937) Autotomy in the brachyuran, *Uca pugnax*. *Biol Bull* 73:155–163
- Honěk A (1993) Intraspecific variation in body size and fecundity in insects - a general relationship. *Oikos* 66:483–492
- Jennings DJ, Boys RJ, Gammell MP (2017) Weapon damage is associated with contest dynamics but not mating success in fallow deer (*Dama dama*). *Biol Lett* 13(11):20170565
- Johnson HE, Bleich VC, Krausman PR (2005) Antler breakage in tule elk, Owens Valley, California. *J Wildl Manag* 69:1747–1752
- Johnson HE, Bleich VC, Krausman PR, Koprowski JL (2007) Effects of antler breakage on mating behavior in male tule elk (*Cervus elaphus nannodes*). *Eur J Wildl Res* 53:9–15
- Jones TM (2001) A potential cost of monandry in the lekking sandfly *Lutzomyia longipalpis*. *J Insect Behav* 14:385–399
- Joseph PN, Emberts Z, Sasson DA, Miller CW (2018) Males that drop a sexually selected weapon grow larger testes. *Evolution* 72:113–122
- Kant R, Minor MA, Trewick SA, Sandanayaka WRM (2012a) Body size and fitness relation in male and female *Diaeretiella rapae*. *Biocontrol* 57:759–766
- Kant R, Trewick SA, Sandanayaka WRM, Godfrey AJR, Minor MA (2012b) Effects of multiple matings on reproductive fitness of male and female *Diaeretiella rapae*. *Entomol Exp Appl* 145:215–221
- Karino K, Niiyama H, Chiba M (2005) Horn length is the determining factor in the outcomes of escalated fights among male Japanese horned beetles, *Allomyrina dichotoma* L. (Coleoptera: Scarabaeidae). *J Insect Behav* 18:805–815
- Karns GR, Ditchkoff SS (2012) Antler breakage patterns in white-tailed deer. *Proc Ann Conf Southeast Assoc Fish Wildl Agencies* 66:114–119
- King BH (2000) Sperm depletion and mating behavior in the parasitoid wasp *Spalangia cameroni* (Hymenoptera: Pteromalidae). *Great Lakes Entomol* 33:117–127
- Lane S, Briffa M (2017) The price of attack: rethinking damage costs in animal contests. *Anim Behav* 126:23–29
- Makatiani JK, Bruce AY, Schulthess F, Takasu K (2013) Reproductive strategies of the larval parasitoid *Microplitis croceipes*. *Entomol Exp Appl* 148:223–233
- Mattlin RH (1978) Population biology, thermoregulation and site preference of the New Zealand fur seal, *Arctocepalus forsteri* (Lesson,

- 1828), on the Open Bay Islands, New Zealand. University of Canterbury, Doctoral dissertation
- Michaud JP, Bista M, Mishra G, Singh O (2013) Sexual activity diminishes male virility in two *Coccinella* species: consequences for female fertility and progeny development. *Bull Entomol Res* 103: 570–577
- Miller CW, Fletcher RJ, Gillespie SR (2013) Conspecific and heterospecific cues override resource quality to influence offspring production. *PlosOne* 8:1–7
- Miller CW, Joseph PN, Kilner RM, Emberts Z (2019) A weapons-testes trade-off in males is amplified in female traits. *Proc R Soc B* 286: 20190906
- Nakatsuru K, Kramer DL (1982) Is sperm cheap? Limited male fertility and female choice in the lemon tetra (Pisces, Characidae). *Science* 216:753–755
- Nolen ZJ, Allen PE, Miller CW (2017) Seasonal resource value and male size influence male aggressive interactions in the leaf footed cactus bug, *Narnia femorata*. *Behav Process* 138:1–6
- O'Neill DJ, Cobb JS (1979) Some factors influencing the outcome of shelter competition in lobsters (*Homarus americanus*). *Mar Behav Physiol* 6:33–45
- Parker GA, Pizzari T (2010) Sperm competition and ejaculate economics. *Biol Rev* 85:897–934
- Proctor DS, Moore AJ, Miller CW (2012) The form of sexual selection arising from male-male competition depends on the presence of females in the social environment. *J Evol Biol* 25:803–812
- R Core Team (2021) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria Retrieved from <https://www.R-project.org/>
- Rubolini D, Galeotti P, Pupin F, Sacchi R, Nardi PA, Fasola M (2007) Repeated matings and sperm depletion in the freshwater crayfish *Austropotamobius italicus*. *Freshw Biol* 52:1898–1906
- Sasson DA, Munoz PR, Gezan SA, Miller CW (2016) Resource quality affects weapon and testis size and the ability of these traits to respond to selection in the leaf-footed cactus bug, *Narnia femorata*. *Ecol Evol* 6:2098–2108
- Simmons LW, Emlen DJ (2006) Evolutionary trade-off between weapons and testes. *Proc Natl Acad Sci U S A* 103:16346–16351
- Simmons LW, Lüpold S, Fitzpatrick JL (2017) Evolutionary trade-off between secondary sexual traits and ejaculates. *Trends Ecol Evol* 32:964–976
- Siva-Jothy MT (1987) Mate securing tactics and the cost of fighting in the Japanese horned beetle, *Allomyrina dichotoma* L. (Scarabaeidae). *J Ethol* 5:165–172
- Small J, Cotton S, Fowler K, Pomiankowski A (2009) Male eyespan and resource ownership affect contest outcome in the stalk-eyed fly, *Teleopsis dalmanni*. *Anim Behav* 78:1213–1220
- Sneddon LU, Huntingford FA, Taylor AC (1997) Weapon size versus body size as a predictor of winning in fights between shore crabs, *Carcinus maenas* (L.). *Behav Ecol Sociobiol* 41:237–242
- Somjee U, Miller CW, Tataric NJ, Simmons LW (2017) Experimental manipulation reveals a trade-off between weapons and testes. *J Evol Biol* 31(1):57–65
- Somjee U, Woods HA, Duell M, Miller CW (2018) The hidden cost of sexually selected traits: the metabolic expense of maintaining a sexually selected weapon. *Proc R Soc B* 285:20181685
- Suzuki Y, Katsuki M, Miyatake T, Okada Y (2015) Relationships among male sexually selected traits in the bean bug, *Riptortus pedestris* (Heteroptera: Alydidae). *Entomol Sci* 18:278–282
- Swierk L, Tennessen JB, Langkilde T (2015) Sperm depletion may not limit male reproduction in a capital breeder. *Biol J Linn Soc* 116: 684–690
- Umbers KDL, Tataric NJ, Holwell GI, Herberstein ME (2012) Ferocious fighting between male grasshoppers. *PlosOne* 7:e49600
- Vessels HK, Bundy CS, McPherson JE (2013) Life history and laboratory rearing of *Narnia femorata* (Hemiptera: Heteroptera: Coreidae) with descriptions of immature stages. *Ann Entomol Soc Am* 106:575–585
- Weir LK, Grant JWA (2010) Courtship rate signals fertility in an externally fertilizing fish. *Biol Lett* 6:727–731
- Wilner D, Greenway EV, Cirino LA, Miller CW (2020) Long-term reproductive success is predicted by sexual behavior and impaired by temporary nutritional stress during sexual maturation. *Behav Process* 175:104122
- Wong BBM, Candolin U (2005) How is female mate choice affected by male competition? *Biol Rev* 80:559–571
- Wong DM, Chou LS, Shiao SF, Bain A (2018) Body size and injury severity associated with mating strategies in male *Philotrypesis taida* fig wasps. *Taiwania* 63:227–231
- Xue L, Noll M (2000) *Drosophila* female sexual behavior induced by sterile males showing copulation complementation. *Proc Natl Acad Sci U S A* 97(7):3272–3275
- Yasuda C, Suzuki Y, Wada S (2011) Function of the major cheliped in male-male competition in the hermit crab *Pagurus nigrofascia*. *Mar Biol* 158:2327–2334

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