



Males missing their sexually selected weapon have decreased fighting ability and mating success in a competitive environment

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Abstract

Intraspecific competition over access to females has led to a large diversity of animal weapons. Generally, the relative size (and presence) of these weapons is positively correlated with mating success, as individuals with the largest weapons often obtain most of the mates. Despite their importance, individuals in some species can lose their weapons. For example, a crab's claw can be dropped to escape life-threatening situations and a beetle's horn can break if it exceeds its mechanical limit. Previous research has shown that individuals missing their weapons are less successful at male-male competition, but few studies have investigated how weapon loss translates to changes in mating behavior and mating success. Here, we investigated how weapon loss affected fighting ability and mating success in the leaf-footed cactus bug *Narnia femorata* Stål (Hemiptera: Coreidae). In this study, males who lost their sexually selected weapons fought in the same manner as intact males, but were five times less likely to establish dominance. Despite this decrease in dominance, 34% of the weaponless males were still able to access females, and the lack of weaponry did not affect a female's willingness to mate. Still, weapon loss ultimately decreased mating success by 37% in a competitive environment.

Significance statement

Sexually selected weapons are important for securing access to mates. Thus, it is often assumed that the permanent loss of a sexually selected weapon dramatically reduces, or even eliminates, an individual's ability to secure matings. In our study, we tested this commonly held assumption. We found that weapon loss decreased both fighting ability and mating success. The observed difference in mating success was not due to female rejection, but instead was likely due to competitive male interactions. These results provide us with a better understanding of the costs associated with permanently losing a sexually selected weapon.

Keywords Autotomy · Fighting behavior · Male-male competition · Mating behavior · Sexual selection

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Introduction

Many of the large and extravagant weapons found throughout the animal kingdom are products of sexual selection, including the antlers of deer and the horns of beetles (Emlen 2008). In these species, males use their weapons in direct, intrasexual competitions to gain access to females and territories (Anderson 1994). Males with larger weapons, as predicted by theory, are more likely to win these contests (fighting asymmetry; Parker 1974), resulting in greater access to mates (Anderson 1994). Still, despite the benefits of possessing a large sexually selected weapon, these structures are sometimes lost. Since weapons are functional traits—being used in male-male combat—they can break if they exceed their mechanical limit (McCullough 2014; McCullough et al. 2014). In addition

to breaking, some species drop (i.e., autotomize) their weapons to escape life-threatening situations (e.g., fiddler crabs (Hoadley 1937), leaf-footed bugs (Emberts et al. 2016)). In either case, the loss of the weapon is permanent if the individual is unable to regenerate a new one. Previous research has shown that the loss of a weapon decreases an individual's fighting ability (O'Neill and Cobb 1979; Berzins and Caldwell 1983; Neil 1985; Smith 1992; Abello et al. 1994; Yasuda et al. 2011; Yasuda and Koga 2016). As a result, it is often assumed that the permanent loss of a sexually selected weapon dramatically reduces, or even eliminates, an individual's ability to secure matings. However, such an assumption fails to consider the possibility that an individual may behaviorally compensate for their missing weapon.

Consider cases in which males are unable to develop (relatively) large weapons. Many of these males are still able to secure some degree of mating success, and often do so by altering their behavior (Gross 1996). For example, in the dung beetle *Onthophagus acuminatus*, weaponless males secure mating opportunities by using a sneaking behavior that allows them to avoid direct male-male contests (Emlen 1997). On the other hand, instead of avoiding contests, some small males actively engage in combat against larger opponents (Morris et al. 1995). Although slightly counterintuitive, theory predicts that using more aggressive tactics (e.g., initiating contests, persisting in contests), under certain scenarios, can result in smaller males winning (Morrell et al. 2005). Thus, given this potential for behavioral compensation, the aim of our study was to determine the effects of permanent weapon loss on fighting strategy, fighting ability, and mating success.

To investigate this aim, we used the leaf-footed cactus bug *Narnia femorata* Stål (Hemiptera: Coreidae; Fig. 1). Males in this species possess sexually selected hind legs, which they use to compete against other males over access to mates and resources (Procter et al. 2012; Nolen et al. 2017). During combat, males use their enlarged, sexually dimorphic, hind legs to kick and squeeze their opponents (Table 1), enabling



Fig. 1 Two *Narnia femorata* males posteriorly aligned abdomen to abdomen, ready to engage in a grapple. Photo credit: CW Miller

them to physically remove other males from a territory (Nolen et al. 2017). Larger males have relatively larger weapons (Allen and Miller 2017) and are more likely to win male-male contests (Procter et al. 2012). Therefore, there is strong evidence to suggest that the hind legs of *N. femorata* are sexually selected weapons (Procter et al. 2012; Nolen et al. 2017). Despite their use as weapons, males can autotomize their hind legs, and once the leg is dropped, it is permanently lost, as *N. femorata* cannot regenerate the limb (Emberts et al. 2016). When limbs are lost through autotomy, individuals in other species are frequently observed, altering their behavior to compensate for the lost limb (Herreid and Full 1986; Stoks 1999; Bateman and Fleming 2006; Cooper 2007; Oliveira et al. 2015). Consequently, weapon loss via autotomy provides an excellent opportunity to determine the extent to which individuals can behaviorally respond to the permanent loss of a weapon.

There are three types of compensatory strategies that males without their weapons might employ to secure access to females. Like males that develop small weapons, males that lose their weapons may establish some degree of dominance by (1) increasing their aggressiveness. This strategy could manifest itself through an increase in contest initiation, contest persistence, or both. Alternatively, individuals that lose their weapon(s) may be able to establish dominance by (2) changing the fighting tactics that they use. Such a strategy has previously been observed in both decapods (O'Neill and Cobb 1979) and stomatopods (Berzins and Caldwell 1983). In *N. femorata*, weaponless males could implement this strategy by decreasing their use of fighting tactics that require both hind legs (grappling; Table 1). Finally, males may still secure access to females while (3) avoiding direct male-male competition, which would suggest that weaponless males implement an alternative reproductive tactic (i.e., a condition-dependent tactic). In our study, we examined the behavior and success of males with and without their weapons to evaluate these three alternatives.

Even if a male acquires access to a female, mating success is still not guaranteed because females could choose not to mate. In *N. femorata*, after a male initiates a mating, the female then determines whether the mating will occur because, if she is unreceptive, she can simply keep her genital plates closed (Gillespie et al. 2014; Cirino and Miller 2017). Consequently, an investigation of male mating success would be incomplete without also considering female choice. In many species, females assess the quality of males before deciding whether to mate (e.g., Hamilton and Zuk 1982; Hill 1991). Since autotomy is a form of injury (i.e., self-induced injury; Emberts et al. 2017), females may differentially mate with intact males over males with missing limbs. Therefore, to investigate the effects of weapons loss on mating success, we need to determine whether weaponless males can access females and whether females are receptive to those males.

Table 1 *Narnia femorata* fighting tactics

Fighting tactic	Definition
Displaying	A raising and widening of the hind limb(s) in the direction of the opponent. This tactic does not require the opponents to physically touch.
Charging	A swift and direct movement toward the opponent, which end in a touching interaction. Note that that this is the only tactic that does not require hind legs.
Kicking	A rapid extension of a hind leg in the direction of the opponent that finishes with physical contact. The aggressor may lunge at his opponent in tandem with the kick in order to ensure contact.
Wrapping	When an individual grips and/or squeeze his opponent with one or two hind legs.
Grappling	A stereotypic behavior in which males aligned abdomen to abdomen to wrap one another with both legs.

These behaviors correspond with coreid fighting tactics already defined in the literature (Nolen et al. 2017), with one exception; we altered the definition of a wrap to include squeezes that only use a single leg (previous definitions required the use of both). Furthermore, we distinguish between stereotypic wrapping, termed grappling (Fig. 1), and non-stereotypic wrapping. We differentiated grappling from wrapping because grappling provides an ideal fighting tactic to investigate behavioral responses to losing a weapon since it involves both hind legs and, due to its stereotypic nature, it is easy to identify regardless of leg presence (Fig. 1)

Since weapon loss is both permanent and frequently observed in the wild (Embets et al. 2016, Embets et al. 2017), we hypothesized that weaponless *N. femorata* males would alter their behavior to compensate for their missing weapons. Nonetheless, since autotomy is a form of injury, we also predicted that males missing their weapons would have lower mating success, as females should prefer intact males over those with missing limbs.

Methods

Rearing of study species

We used first generation lab-reared individuals for our experiment. Populations were founded in July of 2015 with wild-caught *N. femorata*, which were collected from Live Oak, Florida (30.26°N, -83.18°W). *Narnia femorata* were reared in deli cups (top diameter 118 mm, bottom diameter 85 mm, height 148 mm) containing *Opuntia mesacantha* ssp. *lata* cladodes (cactus pads) and fruit collected from the same location throughout the experiment. Nymphs were reared in groups of 5–10 and checked daily, until their terminal molt. Upon becoming adults, individuals were placed into their own deli cup. Each adult was then given 21 days to reach sexual maturity. Individuals that had been in the adult stage longer than 28 days were not used.

Experimental design

Unlike the sexually selected horns of some beetles, the sexually selected trait in *N. femorata* (i.e., their hind legs) is not just limited to male-male combat, but also serves a locomotive function. Thus, it would be imprudent for us to ignore the concurrent negative effects that losing a leg might also have

on fighting and mating outcomes. To address this complexity, we induced limb loss in both mid legs (i.e., a non-sexually selected leg) and hind legs (i.e., a sexually selected leg) to investigate the effects of losing a sexually selected weapon on fighting ability and mating success. Specifically, we randomly placed focal males into one of five treatments ($n = 48$ per treatment): all legs present, missing a single mid leg, missing a single hind (i.e., sexually selected) leg, missing two mid legs, and missing two hind (i.e., sexually selected) legs. Then, each focal individual was randomly assigned to an unrelated male with all of his legs, henceforth, the rival male. Thus, each trial consisted of a unique, random, intact male (the rival) and a focal male. One day before fights occurred, we marked the focal and rival males with paint pens (Elmer's Paint Markers) to distinguish them from one another. Thus, it was not possible to record data blind because our study involves following a focal individual. Also, at this time, we induced autotomy in focal males according to treatment. Autotomy was induced by gripping the leg with reverse action forceps for a few seconds, while the insect was in contact with a piece of wood (Embets et al. 2016). On the day of experimentation, paired focal and rival males were placed into an arena which consisted of a deli cup containing a single planted *O. mesacantha* ssp. *lata* cactus with an attached fruit. Once both males were added, we began behavioral observations, live, for the next 4 h. Since behavioral interactions are both stereotypic and relatively rare, we had a single observer conducted up to 10 trials concurrently.

During behavioral observation, we quantified whether fighting occurred, the fighting tactics used, and ultimately assigned the dominant individual on the basis of these observations. To do this, we defined the following intrasexual interactions: displaying, charging, kicking, wrapping, and grappling (Table 1). If any of these defined tactics (e.g., charging, kicking, grappling) resulted in an opponent retreat, then the aggressor was awarded a single dominance point. After

experimentation, following the same protocol as Procter et al. (2012), the number of dominance points accrued by each male (focal and rival) was summed and the individual with the greatest number of dominance points was considered the dominant male. In the case of ties, dominance was not assigned.

Two hours into the live observation, we added an unrelated, sexually mature female and began to quantify intersexual interactions (specifically, mating and mating attempts), while continuing to evaluate dominance, for the final 2 h. Mating in *N. femorata* is highly stereotypic. Males will initiate mating by mounting a female and aligning his genitals with hers (i.e., male mating attempt). Once aligned, he then presses his intromittent organ against her genital plates. Should the female be receptive, she will open her genital plates, at which point the male will dismount and turn himself away from the female while maintaining genital contact (i.e., mating). If the female is unreceptive, she can flee, kick, and/or simply keep her genital plates closed. In all cases, the male would be unsuccessful in mating. Therefore, we considered female rejection to occur if a male mounted a female (i.e., attempted mating), but was unsuccessful at mating (Gillespie et al. 2014; Cirino and Miller 2017).

Following each trial, all individuals were photographed using a digital camera (Canon EOS 50D) attached to a dissecting microscope (Leica M165 C). Then, body size (pronotal width) was measured to the nearest micrometer using ImageJ software (v.1.46).

Ethical note

Narnia femorata naturally autotomize their front, mid, and hind legs to escape predation and entrapment (Emberts et al. 2016, 2017). In fact, up to 13% of individuals in the wild are missing at least one limb, with some missing up to three (Emberts et al. 2016). In the lab, autotomy is never forced; we simply initiate self-induced autotomy by holding an individual's limb for a few seconds. Like autotomy, male-male competition is also a naturally occurring behavior in *N. femorata*. However, to reduce competitive interactions, adult males were only paired during experimental trials. Finally, all individuals were treated as humanely as possible by providing them with ideal rearing conditions throughout the study.

Statistical analyses

To investigate the effects of limb loss on dominance and fighting behavior we conducted planned, a priori, contrasts in the context of generalized linear models (GLMs). Since we specifically hypothesized that the loss of the hind, sexually selected legs would affect fighting ability and behavior we conducted three contrasts: contrast 1—individuals missing hind leg(s) versus individuals with all of their legs, contrast 2—

individuals missing mid leg(s) versus individuals with all of their legs, and contrast 3—individuals missing hind leg(s) versus individuals missing mid leg(s). In all of our models, we also included body size (i.e., pronotal width of focal individual) and the difference in body size between the focal and rival as covariates. Both traits were included as covariates because previous work in this species has shown that body size and the difference in body size can have a significant effect on fighting outcomes and/or behaviors (Procter et al. 2012; Nolen et al. 2017).

First, to investigate whether limb loss affects the propensity to engage in male-male contests, we compared the frequency of fighting encounters (i.e., whether at least one fighting behavior, including a display, occurred per pair, yes/no) across the contrasted treatments using a logit-link function and assuming a binomial distribution (i.e., a GLM for binary data). Then, given that there was a fighting encounter, we investigated whether weapon loss affected fighting outcomes by comparing dominance (yes/no) of the focal male across the contrasted treatments. Using this same subset of the data, we also investigated whether limb loss affected male competitive behavior. Specifically, we asked whether the propensity to grapple (yes/no) or the propensity to charge (yes/no) varied across the contrasted treatments. These two tactics were explicitly chosen because they can easily be identified by an observer even if a male is missing both of his hind legs. For example, due to the stereotypic nature of a grapple (Fig. 1), an observer can determine if a weaponless male is attempting to grapple when the weaponless male aligns abdomen to abdomen with his rival. Finally, we also investigated whether limb loss affected fighting persistence (i.e., the number of fighting behaviors that occurred per pair) across our contrasted treatments using a log-link function and assuming a Poisson distribution. Having a measure of an individual's decisions to flee (i.e., persistence) helps us understand the extent to which autotomy affects the decision making process during fights. We also explicitly investigated the correlation between body size and fighting persistence (i.e., contest duration) for winners and losers (Arnott and Elwood 2009) to place the behavior of *N. femorata* in the context of previous literature on give-up decisions in male-male combat.

Next, we conducted similar analyses (i.e., GLMs with contrasts) to investigate the effects of limb loss on mating success (mated yes/no). Then, to better understand any differences in mating success, we investigated whether the loss of hind legs and/or dominance affected male mating attempts (mount yes/no) and/or female choice (accept/reject).

Although differences in losing one limb versus losing two is not the main focus of this manuscript, to ease curiosities and develop hypotheses, we also investigated whether the number of limbs lost affected fighting ability and mating success. For these analyses, we used GLMs with contrasts, but contrasted

those missing two limbs against those missing just one. All analyses were conducted in R v.3.3.1 (R Core Team 2016).

Data availability The datasets generated during and/or analyzed during the current study are available from the corresponding author on reasonable request.

Results

To gain a better understanding of how weapon loss affects fighting ability and mating success, first, we describe the outcomes and behaviors of the focal individuals with all of their legs to establish a comparative baseline. Recall that focal males were always paired with an intact (non-autotomized) rival. Of the 48 focal males with all their legs, 18 (38%) had at least one fighting encounter. Of those 18, the focal individual established dominance in 10 (56%; Fig. 2). Furthermore, 5 of the 18 focal males (28%) engaged in grappling at least once, while 2 of the 18 charged at least once (11%; Fig. 3). With regard to mating, 25 (52%) of the focal males attempted to mate (i.e., mounted), but only 20 (42%) mated (Fig. 2). Therefore, females rejected 20% of the males that attempted to mate.

When we contrasted focal individuals missing their mid leg(s) against focal individuals with all of their legs (contrast 2), we found no evidence to suggest that the loss of a mid leg affected any of the investigated response variables (Figs. 2 and 3 and Table 2).

Effects of losing a weapon on fighting ability and behavior

The loss of a sexually selected weapon affected a male's dominance, but not fighting behavior. We found that focal males missing their sexually selected hind legs had a lower probability of establishing dominance (9%) compared to those missing mid legs (45%; contrast 3 $\chi_1^2 = 11.113$, $p < 0.001$) and those with all of their legs (56%; contrast 1 $\chi_1^2 = 17.546$, $p < 0.001$; Fig. 2). Nonetheless, loss of hind legs did not have a significant effect on fighting behavior. Individuals missing hind legs were just as likely to engage in male-male competition as individuals with all of their legs (contrast 1 $\chi_1^2 = 0.362$, $p = 0.547$) and individuals missing mid legs (contrast 3 $\chi_1^2 = 1.132$, $p = 0.287$; Fig. 3). Furthermore, the proportion of individuals that used a grapple, a fighting tactic that incorporates both hind legs, did not vary across the contrasted treatments (contrast 1 $\chi_1^2 = 1.115$, $p = 0.291$; contrast 3 $\chi_1^2 = 2.482$, $p = 0.115$; Fig. 3). The proportion of focal individuals that used a charge was similar as well (contrast 1 $\chi_1^2 = 0.010$, $p = 0.920$; contrast 3 $\chi_1^2 = 0.038$, $p = 0.845$; Fig. 3). Moreover, there was no observable difference in fighting persistence. Males

missing their sexually selected hind legs were just as likely to persist in fights as males missing mid legs (contrast 3 $\chi_1^2 = 2.413$, $p = 0.120$) and males with all of their legs (contrast 1 $\chi_1^2 = 0.405$, $p = 0.524$). Fighting persistence did however positively correlate with body size for subordinate males ($\chi_1^2 = 37.56$, $p < 0.001$), although the relationship between persistence and body size was not present for males that became dominant ($\chi_1^2 = 1.456$, $p = 0.228$; Fig. 4).

Effects of losing a weapon on mating success

The loss of a sexually selected weapon also reduced a male's probability of mating. Focal males missing hind legs mated less than those missing mid legs (contrast 3 $\chi_1^2 = 7.003$, $p = 0.008$) and those who had all their legs (contrast 1 $\chi_1^2 = 6.128$, $p = 0.013$; Fig. 2). Still, approximately 25% of males missing hind legs secured a mating (compared to approximately 40% for those missing their mid legs and those with all their legs).

A decrease in mating success could reflect that weapon loss (1) decreased male mating attempts or (2) increased female rejection, or both. In our study, there was no evidence to suggest that weapon loss increased female rejection (i.e., there was no variation among treatments in female choice; contrast 3 $\chi_1^2 = 1.412$, $p = 0.235$; contrast 1 $\chi_1^2 = 0.353$, $p = 0.552$). Instead, we found that the loss of sexually selected hind legs reduced a male's mating attempts compared to those who lost mid legs (contrast 3 $\chi_1^2 = 6.001$, $p = 0.014$) and those who had all of their legs (contrast 1 $\chi_1^2 = 6.272$, $p = 0.012$; Fig. 2), as only 34% of these males attempted to mate compared to approximately 50% of males in other treatments.

As hypothesized in Nolen et al. (2017), we also found that *dominance* explained variation in attempted mating ($\chi_1^2 = 6.881$, $p = 0.009$) and tended to explain variation in mating success ($\chi_1^2 = 3.523$, $p = 0.061$) when we considered all competing males together. Therefore, our mating observations could be a result of dominance interactions, not the loss of weaponry per se. Thus, we statistically controlled for dominance to tease apart the direct effects of weapon loss on male mating behavior and success by adding fighting status as a covariate into our models. When doing so, weapon loss, itself, did not influence attempted matings (contrast 1 $\chi_1^2 = 0.404$, $p = 0.525$; contrast 3 $\chi_1^2 = 2.121$, $p = 0.145$) nor mating success (contrast 1 $\chi_1^2 = 0.147$, $p = 0.701$; contrast 3 $\chi_1^2 = 2.538$, $p = 0.111$).

Effects of losing one limb versus two

The number of limbs lost (i.e., 1 limb versus 2) did not have an effect on the investigated outcomes (i.e., dominance and mating success), but we did find that individuals missing two

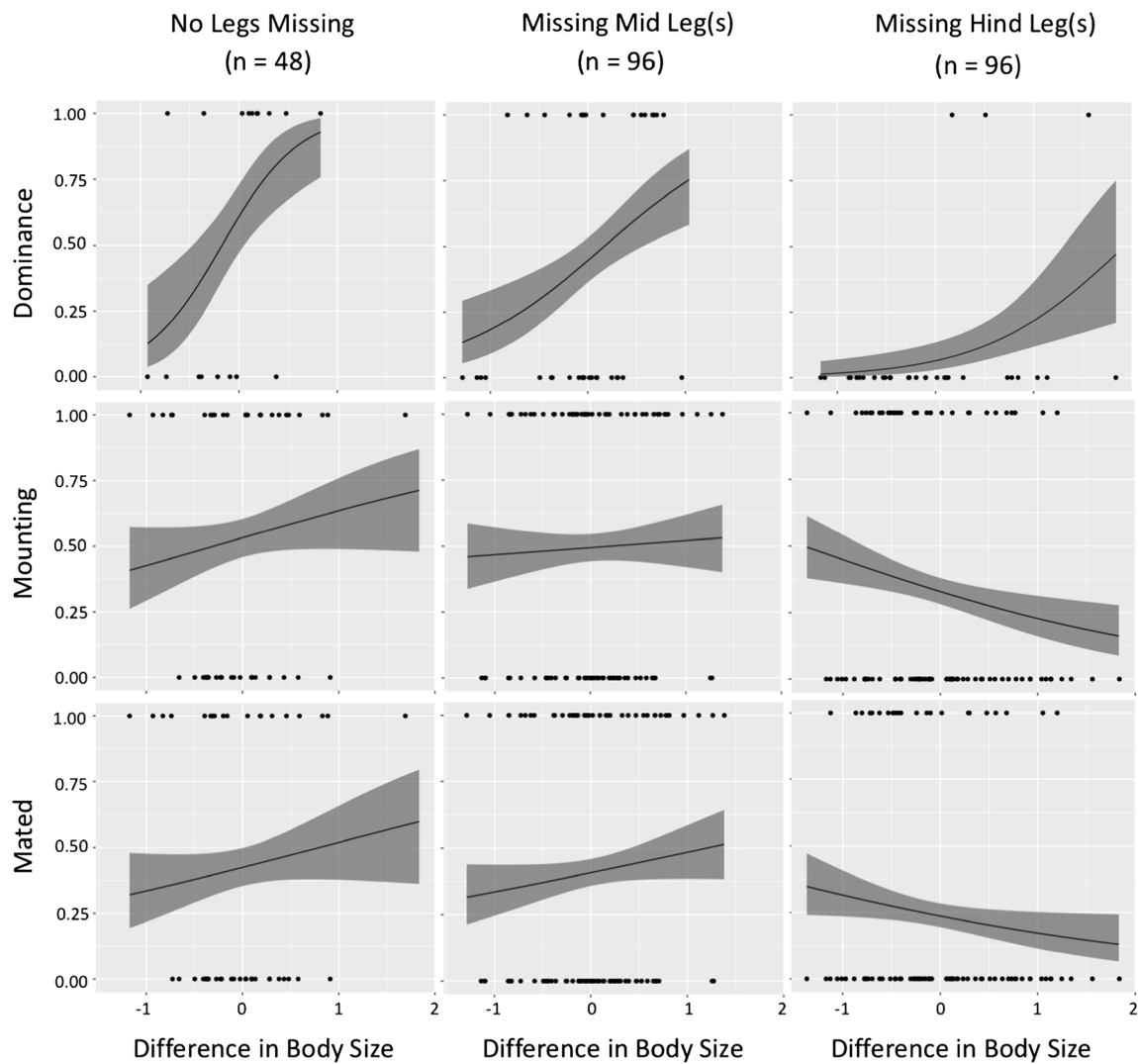


Fig. 2 The effects of losing a weapon on fighting ability and mating success. Loss of a weapon in *N. femorata* significantly decreases a male's fighting ability (i.e., dominance), mating attempts (i.e., mounting), and mating success (i.e., mated). Loss of a middle leg had no effect on these factors (Table 1). Females did not discriminate against males across the contrasted treatments. Predicted proportions and standard errors displayed were derived from a generalized linear model with a

logit-link function and the assumption of a binomial distribution taking difference in body size into consideration. This simplified model was used to help visualize the data. All models were constrained within the bounds of the x axis (i.e., difference in body size (mm)) to avoid extrapolation. Only a subset of the data was used to investigate fighting ability because we were unable to assess dominance for each trial

limbs were less likely to grapple than individuals missing one ($\chi^2_1 = 3.920, p = 0.048$; Table S1).

Discussion

Males who lost their sexually selected weapons were more likely to lose contests. Despite this handicap, males missing their weapons were just as likely to engage in male-male competition, persist once the competition started, and even used fighting tactics that appear to require both hind legs. These results reveal a surprising lack of plasticity in *N. femorata*

fighting behavior. Similarly, loss of weaponry, per se, did not affect a male's mating behavior. However, subordinate males were less likely to attempt to mate (see also Nolen et al. 2017) and males without their weapons were more likely to be subordinate. Consequently, weapon loss influenced a male's pursuit of females, which ultimately decreased male mating success in a competitive environment. These results support the assumption that the permanent loss of a sexually selected weapon reduces an individual's ability to secure matings. However, our results refute the claim that the loss of a sexually selected weapon removes an individual from the mating pool, as 25% of the males who lost their weapons still secured a mating.

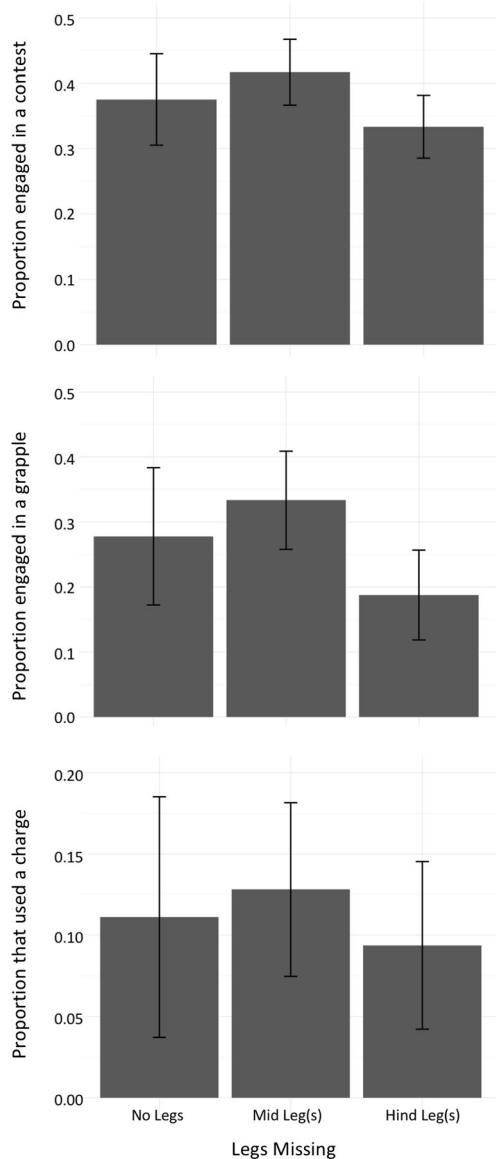


Fig. 3 Lack of plasticity in fighting behavior. Loss of a sexually selected weapon did not affect a male's propensity to engage in a fight nor did it affect a male's fighting tactic. Displayed is the proportion of focal individuals that engaged in fighting, grappling, and charging \pm SE

Compensatory behavior has frequently been observed following autotomy (Herreid and Full 1986; Stoks 1999; Bateman and Fleming 2006; Cooper 2007; Oliveira et al. 2015), and likely mitigates the costs associated with losing a limb. As such, we hypothesized that weaponless males would alter their behavior to compensate for their missing weapon(s). We found that males without their weapons behaved in the same manner as males that possessed their weapons, highlighting that compensatory behavior does not always succeed autotomy.

There are several hypotheses that might explain the lack of observed fighting plasticity. It is possible that weaponless males did not alter their behavior because they were unable

Table 2 Results of contrast 2—the comparison between males missing middle legs and intact males

Variables	χ^2	df	p
Mounting	0.246	1	0.620
Rejection	0.087	1	0.768
Mating	0.102	1	0.750
Dominance	1.649	1	0.199
Engage in fight	0.074	1	0.786
Grapple	0.048	1	0.828
Charge	0.002	1	0.962
Persistence	0.331	1	0.565

Loss of middle leg(s) did not affect any of the investigated outcomes and behaviors relative to intact (non-autotomized) individuals

to perceive their (new) fighting ability prior to interactions. This hypothesis is pertinent because we only investigated the males' first fighting opportunity post-autotomy. Moreover, since our results suggest that *N. femorata* make their fighting decisions following pure-self-assessment models (Fig. 4; Arnott and Elwood 2009), like the energetic war of attrition (Payne and Pagel 1996), it makes sense that dropping a weapon would not necessarily alter a male's first fighting interaction. Fighting decisions under pure self-assessment models are based on a cost threshold that is established before fighting even begins and does not change during an interaction. In such cases, we would not expect to observe a change in fighting behavior until subsequent fighting interactions. Alternatively, male *N. femorata* may primarily use their body size, as opposed to their weapon size, to assess their fighting ability, as is commonly found across species (Anderson 1994). Under this scenario, the loss of a hind leg may not alter a male's decision to engage, persist, and grapple in competitions because their body size is unaffected (discussed in Yasuda and Koga 2016). It is also possible that males accurately assess their fight ability, but did not alter their behavior because the cost of fighting is low, while the benefits are high. In such instances, weaponless males would still be predicted to engage in male-male competitions (Morrell et al. 2005). Finally, weaponless males in their natural environment may be able to avoid conflict by seeking territories that are unoccupied (Booksmythe et al. 2009). Under this scenario, there would be little to no selection for males to evolve compensatory fighting behaviors. Still, in this study, males missing weapons were able to secure dominance 9% of the time (as compared to ~50% for males that possessed their weapons) without changing any of the investigated fighting behaviors.

Success in male-male competition may not completely determine mating opportunity. Therefore, we also investigated how weapon loss affected a male's mating behavior. Like fighting behavior, weapon loss, per se, did not affect mating behavior. However, dominance did (see also Nolen et al.

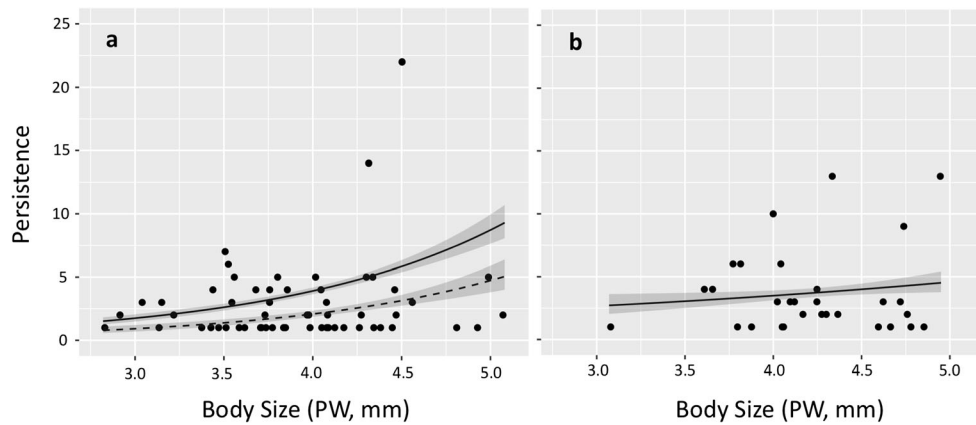


Fig. 4 Body size explains variation in contest duration for subordinate males (a), but not dominant ones (b). Predicted trend lines and standard errors were derived from generalized linear models with a log-link function and the assumption of a Poisson distribution. Solid trend lines include

all data points, while the dashed trend line excludes our outlier (persistence = 66, body size = 4.41 mm; data point not displayed). Including or excluding the outlier did not affect our conclusions. Persistence is the total number of fighting interactions over the 4-h duration

2017). Compared to a subordinate male, a dominant male was twice as likely to attempt a mating. Since weaponless males were less likely to be dominant, they were also less likely to attempt a mating. Therefore, weapon loss appears to indirectly influence mating behavior. We should take some caution in this assertion because statistically controlling for dominance also reduced our sample size (from $n = 238$ to $n = 88$) since we were unable to assess dominance in every trial. Regardless, losing a weapon ultimately reduces a male's mating opportunities in a competitive environment.

Female mating behavior could have also affected a male's mating success because females could choose not to mate. In our study, neither the presence of weaponry nor dominance status affected female choice. However, females clearly make mating decisions in *N. femorata* (e.g., Gillespie et al. 2014), and limb loss provides an ideal opportunity to understand whether injury and asymmetry affect female choice. In several species, females are more likely to mate with males that have symmetrical traits (e.g., zebra finch, swordtail fish; Swaddle and Cuthill 1994; Morris 1998). In general, male *N. femorata* (with all their legs) are fairly symmetric (Allen and Miller, unpublished data). However, up to 9% are missing a single leg in the wild (Embets et al. 2016), making them radically asymmetric. When we investigated female choice for symmetrical males (loss of two legs versus one from the same position), we found no evidence that females differentially mated with symmetric males over asymmetric ones. Besides asymmetry, females may also assess the health and/or quality of males before deciding whether to mate (e.g., Hamilton and Zuk 1982; Hill 1991), and since autotomy is a form of injury (i.e., self-induced injury; Embets et al. 2017), females may discriminate against males with autotomized limbs. However, *N. femorata* females did not differentially discriminate among males from our different treatments.

In summary, weapon loss decreased both fighting ability and mating success, as weaponless males did not behaviorally compensate for their missing limbs. These intriguing results suggest directions for future investigation. Future studies should determine whether the differences in mating success, such as those observed here, result in similar differences in reproductive success. The distinction between reproductive success and mating success is particularly important when you consider that both the focal and rival male mated with the female in 11% of the trials. Consequently, postcopulatory competition could play a major role in determining an individual's fitness. For example, weaponless/subordinate males may allocate more sperm per mating, potentially increasing their relative reproductive success (Joseph et al. 2018; Somjee et al. 2018). Future studies should also determine whether there are temporal or experiential consequences to permanently losing a weapon. It is possible, for example, that previous fighting experiences affect the subsequent fighting outcomes and behaviors of weaponless males (Hsu et al. 2006). These additional studies would ultimately contribute to our understanding of the costs associated with permanently losing a sexually selected weapon.

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Compliance with ethical standards

Ethical approval All applicable international, national, and/or institutional guidelines for the care and use of animals were followed.

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