



Original Article

Damage from intraspecific combat is costly

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Received 4 March 2021; revised 11 May 2021; editorial decision 1 July 2021; accepted 5 July 2021.

When individuals engage in fights with conspecifics over access to resources, injuries can occur. Most theoretical models suggest that the costs associated with these injuries should influence an individual's decision to retreat from a fight. Thus, damage from intraspecific combat is frequently noted and quantified. However, the fitness-related costs associated with this damage are not. Quantifying the cost of fighting-related damage is important because most theoretical models assume that it is the cost associated with the damage (not the damage itself) that should influence an individual's decision to retreat. Here, we quantified the cost of fighting-related injuries in the giant mesquite bug, *Thasus neocalifornicus*. We demonstrate that experimentally simulated fighting injuries result in metabolic costs and costs to flight performance. We also show that flight costs are more severe when the injuries are larger. Overall, our results provide empirical support for the fundamental assumption that damage acquired during intraspecific combat is costly.

Key words: damage, fight, injury, intraspecific competition, intrasexual competition, male–male combat.

INTRODUCTION

Many animals fight with conspecifics over access to limited resources (e.g., food, shelter, and mates; Smith and Price 1973; West-Eberhard 1983; Rico-Guevara and Hurme 2019). During these fights injuries can occur. Examples include bite wounds in lizards (Lailvaux et al. 2004), puncture wounds in shrimp (Rojas et al. 2012), and scratch wounds in lemurs (Kappeler 1997). Most theoretical models assume that such injuries influence an individual's decision to retreat from a fight, which ultimately influences who wins (Parker and Rubenstein 1981; Hammerstein and Parker 1982; Enquist and Leimar 1983; Payne 1998; Lane and Briffa 2017; Palaoro and Briffa 2017). Experimental studies have recently found support for this assumption (Emberts and Wiens 2021). Damage (that is accrued during combat) is thought to influence an individual's willingness to persist in a fight because damage is assumed to have a fitness-related cost (Parker and Rubenstein 1981; Hammerstein and Parker 1982; Enquist and Leimar 1983; Payne 1998). Thus, understanding the costs associated with fighting-related damage is crucial to understanding intraspecific contests. Despite their importance, much remains unknown about the costs associated with fighting-related injuries.

The assumption that damage from intraspecific combat is costly is a reasonable one. Acute injuries can result in reduced function of damaged body parts, blood loss, and energetically expensive immune responses (Lochmiller and Deerenberg 2000; Ardía et al.

2012). These injuries could reduce an individual's ability to escape predators (e.g., Krause et al. 2017) and secure mates (e.g., Salvador et al. 1995; Emberts et al. 2018). Thus, they may have serious fitness consequences. Nevertheless, the severity of the costs associated specifically with fighting-related injuries are largely unstudied. This is an important omission because it is these costs (not the injuries per se) that are theorized to influence an individual's fighting behavior (Parker and Rubenstein 1981; Hammerstein and Parker 1982; Enquist and Leimar 1983; Payne 1998; Lane and Briffa 2017; Palaoro and Briffa 2017). Thus, it is crucial to test if combat-related damage is costly and determine whether some injuries are more costly than others.

To investigate the costs of damage from intraspecific fighting, we used the giant mesquite bug, *Thasus neocalifornicus* (Insecta: Hemiptera: Coreidae, Figure 1). Male *T. neocalifornicus* use their enlarged and spined hind legs in fights with conspecific males over access to territories (Emberts and Wiens 2021). During these fights, males can puncture their rival's forewings (Figure 1; see also Emberts and Wiens 2021). Similar forewing punctures are not found in coreids that lack sexually selected weapons (Emberts, Hwang, et al. 2021), suggesting that this type of damage (in males) is unique to intrasexual combat.

There is some a priori evidence that forewing punctures are costly. First, melanization often occurs around the wounds (Emberts and Wiens 2021), indicating a metabolically expensive immune response (Cerenius and Söderhäll 2004; Ardía et al. 2012). Such an immune response may temporarily increase an individual's resting metabolic rate (RMR; Ardía et al. 2012). Second, damage occurs on their wings (Figure 1), which may

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Figure 1

Male *Thasus neocalifornicus* (A) use their weaponized hind legs in fights with other males over access to territories (Embets and Wiens 2021). During these fights, males will press their tibial spines into their opponents wings, resulting in puncture wounds. (B) Note that wing punctures are located in the top half of the wing (i.e., the corium). The maximum diameter of the puncture wounds shown in B (from left to right) are 0.4 mm, 1.1 mm, and 2.2 mm. Wing photos in this figure and Figures 2 and 3 were modified (i.e., had their backgrounds removed) so that the puncture wounds could more easily be visualized.

reduce flying ability (Combes et al. 2010; Mountcastle et al. 2016). Thus, we predicted that damage associated with male–male competition should have both metabolic and locomotory costs. Moreover, puncture size varies considerably (Embets, Hwang, et al. 2021; Figure 1). Thus, we also predicted that larger punctures should be more costly than smaller ones. To investigate these predictions, we first tested whether damage influences an individual's metabolic rate during a resting phase (i.e., standard or RMR; Mathot and Dingemanse 2015). We then tested whether forewing damage influences how far an individual can fly and if larger punctures had greater impact on flying performance.

MATERIALS AND METHODS

Experiment 1: metabolic costs

Animal collection and husbandry

Adult male *T. neocalifornicus* used for this first experiment were collected in Santa Cruz County, AZ (south of Tubac; 31.5294, –111.0218). Individuals were collected by hand September 8–16, 2020, given the availability of a FoxBox Respirometry System (Sable Systems Hendersons, Las Vegas, NV) at that time.

Some individuals had minor wing damage before the experimental treatment. This should not be problematic because metabolic costs of injury were assessed using a before-and-after experimental design (see below). All individuals had their pronotums uniquely marked with paint pens and permanent markers for identification (regardless of treatment, see below). Collected individuals were housed together in large, mesh insect-rearing containers (305 × 305 × 607 mm; L × W × H) for up to 96 h (up to 20 individuals per container) at room temperature (~26 °C) and provided with several fresh cuttings of velvet mesquite (*Prosopis velutina*) for food. Interactions within the rearing container are limited under these conditions (e.g., males do not appear to fight, see Embets and Wiens 2021). Thirty minutes before measuring CO₂ production, individuals were moved into separate containers without food or water.

Measuring RMR

Flow-through respirometry was used to measure the rate of CO₂ production as a proxy for RMR for each individual ($n = 27$). The CO₂ analyzer was calibrated using CO₂ free dry air and 2000 ppm CO₂ in N₂. Incurrent air was pulled through the apparatus and first scrubbed of moisture using a silica bead column, then scrubbed of CO₂ and further moisture using an ascarite and drierite column (WA Hammond Drierite Company, Xenia, OH). This dry CO₂-free air then passed through an in-built pump and flow control system (FoxBox) before being passed through a custom glass cylindrical insect chamber (50 ml) and finally through the CO₂ analyzer with a sampling frequency of 1 Hz. Gas circulation between instruments occurred through 3 mm diameter plastic tubing and connecting plastic valves (Bevaline-IV, Cole Parmer, Vernon Hills, IL).

An individual was placed inside the insect chamber and a measurement was taken once it stopped moving and readings stabilized, a process that took approximately 8 min (Lighton 2008). The chamber was placed in a dark foam box with a viewing window to minimize disturbance and allow individuals to reach a phase where movement ceased. Flow rates were set to maximize the temporal resolution of CO₂ production and detectability at a standard temperature and pressure (200 ml/min). Temperature was checked throughout the trial with readings from a separate thermometer (Oregon Scientific thermometer) placed beside the measurement chamber, but note that we do not have complete temperature data for two individuals (Embets, Hwang, et al. 2021).

Respirometry data were extracted from Expedata software (v1.9.27; Sable Systems), which received signals directly from a built-in analog-to-digital converter in the FoxBox. Molar rates of CO₂ production were then calculated from raw measures of CO₂ (ppm) using the known flow rate and variables in the Ideal Gas Law equation:

$$\text{CO}_2 = \frac{[P \times \text{FR} \times (\text{Fi} - \text{Fe})]}{R \times T}$$

Where CO₂ is the rate of CO₂ production (mols/min), FR is the flow rate (200 ml/min), Fi and Fe are the fractional concentrations of incurrent and excurrent CO₂, respectively, P is the pressure (1 standard

atmosphere), R is the gas constant at standard temperature and pressure ($0.08206 \text{ L atm K}^{-1}\text{mol}^{-1}$), and T is the temperature (Kelvin). We multiplied moles of CO_2 by the molar volume of an ideal gas (22400 ml/mol at standard temperature and pressure) to get volume of CO_2 (ml/s) and multiplied this by 21.1 J/ml and divided by a respiratory quotient (RQ) of 1 to get our respiration rate in J/s or Watts (Lighton 2008). An RQ of 1 was used for this conversion because *T. neocalifornicus*, like many hemipterans, is a sap feeder (Olivier-Espejel et al. 2011), indicating a high carbohydrate diet (sensu Somjee et al. 2018). Baseline measurements with empty chambers were taken at the beginning and end of each run and subtracted from periods of stable minimal readings when individuals were not visibly moving to maximize accuracy and account for potential sensor drift (Lighton 2008).

After measuring RMR, individuals were randomly assigned to one of two treatments using a random number generator: a comparative baseline treatment ($n = 13$) or an experimental manipulation ($n = 14$). Each individual in the experimental manipulation treatment received two puncture wounds, each 3 mm in diameter. One puncture was placed in the corium of each forewing (one per side), where damage from male–male combat normally occurs (Figure 1). Moreover, two puncture wounds were used as opposed to one because wild-caught *T. neocalifornicus* males that are damaged rarely have a single puncture wound and most have seven or more (Emberts, Hwang, et al. 2021). Finally, the puncture wounds were 3 mm in diameter because previous studies found that wild-caught *T. neocalifornicus* males can have puncture wounds $>3 \text{ mm}$ in diameter (maximum = 3.150 mm ; Emberts, Hwang, et al. 2021). The average diameter of puncture wounds in wild-caught male *T. neocalifornicus* is 0.440 mm (note: measured individuals in that study were from the same site or nearby those used here). Therefore, 3 mm puncture wounds are relatively large but still biologically relevant. Wounds were made using a XOOL leather hole puncher (i.e., experimentally induced) to mimic those received during a fight (Supplementary Figure S1). Wounds were made experimentally so that we could isolate the costs associated with the damage itself. RMR was measured (for a second time) approximately 30 min after injury because our previous observations suggested that if there was an energetic cost (associated with the injury) we would most likely see it at this time (Somjee et al. 2018). Individuals in the comparative baseline treatment were not punctured, but were handled similarly to those that were. Specifically, these control individuals had their forewings spread and placed on the hole puncher for 3 s (per forewing). However, these individuals did not actually have their wings punctured. The same methods described above were used to measure RMR for the second time and they were taken within 24 h of the first measurement. The first measurement was then subtracted from the second to calculate each individual's change in RMR. Individuals were then massed to the nearest hundredth of a gram using a TPO-100 digital pocket scale. However, three individuals were not massed because the scale was unavailable. Pronotal width was also measured to the nearest hundredth of a millimeter using a Mitutoyo digital caliper. Pronotal width is a widely used proxy for body size in this clade (Proctor et al. 2012; Emberts et al. 2020).

Experiment 2: locomotory costs

Animal collection and husbandry

Adult male *T. neocalifornicus* used for the second experiment were collected near those for the first, in Pima County, Arizona (SE of Green Valley: $31.7921, -110.8813$; S of Vail: $31.9640, -110.6729$). All individuals were collected by hand between 23 June and 8

July 2020. This is when adult *T. neocalifornicus* begin to emerge (Emberts and Wiens 2021), making it easier to find fully sclerotized males without wing damage. Individuals were marked, measured (pronotal width), housed, and fed as described above.

Flight trials

Three hours before experimentation, each individual was randomly assigned (with a random number generator) to one of five treatments ($n = 20$ per treatment). In these treatments they received either: (i) no wing punctures (i.e., comparative baseline) or two wing punctures (one per wing) that were either: (ii) 1 mm (diameter), (iii) 2 mm, (iv) 3 mm, or (v) 4 mm. The size, number, and location of punctures (on the corium) followed the reasoning explained above. The 1 mm punctures were made using a 20 gauge sewing needle, whereas 2, 3, and 4 mm punctures were made using a XOOL leather hole puncher. Individuals in the comparative baseline treatment were not punctured but were handled similarly to those that were (see above).

Two hours after their treatment, individuals participated in a flying trial. These trials were conducted outside on a manicured grass field (Supplementary Video S1) in a randomized order. To initiate flight, individuals were held in an observer's hand 1.5 m above the ground. This was a height at which individuals were found naturally (although they can also be found much higher). Individuals were then lightly tapped by the observer to initiate a flight response. Thus, these trials may be considered an anti-predatory response to a human predator. After individuals took off, the horizontal distance from the observer's hand to their landing location was recorded in meters with a Champion Sports open reel measuring tape. Most individuals landed on the ground. However, for individuals that flew more than 23 m, it was possible for them to land on an object (e.g., a tree, a fence). When this happened, the horizontal distance from the starting location to the landing site was recorded. Flying trials were conducted between 10 AM and 7 PM at air temperatures from 31 to 38 °C. Time and temperature were recorded for use as factors in the statistical analyses.

Statistical analyses

Experiment 1: metabolic costs

First, we tested whether the difference between an individual's first and second RMR measurements (i.e., the dependent variable) could be explained by treatment (i.e., whether they received experimental wing punctures, independent variable) using a generalized linear model (GLM). This model also included pronotal width (body-size proxy) and air temperature (when measuring RMRs) as covariates. We confirmed that including or excluding these covariates produced qualitatively similar results (Supplementary Tables S1 and S2), as did using an alternative body-size proxy (i.e., mass; Supplementary Tables S1 and S3). Given that individuals in our comparative baseline treatment appeared to have slightly lower RMRs after their sham treatment (see Results), we also conducted some follow-up analyses. Specifically, we conducted two paired t -tests (because each individual was measured twice) to determine whether (1) the decrease observed in our comparative baseline treatment was statistically significant and (2) whether wing damage itself significantly increased an individual's RMR.

Experiment 2: locomotory costs

We then examined whether wing damage (i.e., treatment, independent variable) influenced how far individuals flew (dependent variable) using another GLM. For this analysis, we included

pronotal width (9.46–14.13 mm), air temperature (31–38 °C), and time of day at the start of the trials (10–18.5 h) as covariates. Given a significant result, we then performed a Tukey pairwise comparison to determine which treatments were responsible for driving the observed effect. We confirmed that including or excluding our covariates produced qualitatively similar results (see Results and Supplementary Tables S4–S7), as did including or excluding the 4 mm treatment (i.e., with punctures larger than in wild populations; see Results and Supplementary Tables S8 and S9). All statistical analyses were conducted in R v 4.0.3 (R Development Core Team 2020).

RESULTS

We found that damage accrued during intrasexual combat can be costly. First, individuals that experimentally received wing punctures appeared to increase their RMR ($t = 2.701$, $df = 24$, $P = 0.014$; Supplementary Table S1; Figure 2). However, visualization of the data (Figure 2) suggested that this significant result may have been driven by individuals in the comparative baseline treatment (which appeared to have lowered their RMR). We confirmed that this was not the case. A paired t -test analysis revealed that individuals in the comparative baseline treatment had similar RMRs before and after receiving the sham treatment ($t = -1.755$, $df = 12$, $P = 0.105$). Moreover, individuals in our experimental manipulation treatment had significantly higher RMR after receiving their wing punctures (paired t -test: $t = 2.227$, $df = 13$, $P = 0.044$). These analyses collectively show that receiving forewing damage increased an individual's RMR.

The presence and severity of wing punctures also influenced how far individuals could fly (Figure 3). Non-damaged individuals (i.e., comparative baseline treatment) flew 60.4 m on average, whereas individuals with 4 mm puncture wounds flew 0.61 m on average (i.e., a 99% reduction; $z = -5.904$, $P < 0.001$; Supplementary Table S6). Individuals with 2 and 3 mm puncture wounds both flew ~24 m on average (i.e., a 60% reduction from non-damaged individuals; 2 mm: $z = -3.501$, $P = 0.004$; 3 mm: $z = -3.766$, $P = 0.002$; Supplementary Table S6). Finally, individuals with 1 mm puncture wounds flew 40.1 m. This distance was not statistically different from our comparative baseline (40.1 m compared with 60.4 m; $z = -1.761$, $P = 0.397$), but was statistically different from individuals with 4 mm puncture wounds (40.1 m compared with 0.6 m; $z = -4.184$, $P < 0.001$; Supplementary Table S6). This latter result showed that the severity of damage influenced flight performance costs.

DISCUSSION

We investigated whether damage accrued during intrasexual combat is costly using the giant mesquite bug, *T. neocalifornicus*. In this species, intrasexual combat frequently results in wing damage (Figure 1; Emberts and Wiens 2021). Thus, we experimentally induced injuries (which mimicked those received during a fight; Supplementary Figure S1) and investigated whether this damage had a metabolic and/or locomotory cost (i.e., two potential indirect fitness costs). First, we found that there was an energetic cost associated with fighting-related injuries. Second, we found that wing damage decreased flying ability and that this performance cost was more severe when puncture wounds were larger. Overall, these results provide empirical support for the fundamental assumption that damage acquired during intraspecific combat is costly and

illustrate that some fighting-related injuries can be far more costly than others.

Understanding the costs associated with intraspecific fighting is crucial because theory suggests that these costs influence contest outcomes and behavior (Parker and Rubenstein 1981; Hammerstein and Parker 1982; Enquist and Leimar 1983; Payne 1998). Costs typically associated with intraspecific combat include energetic consumption (Smith and Taylor 1993; Hack 1997; Rovero et al. 2000), reduced function of damaged body parts (Berzins and Caldwell 1983; but see Johnson et al. 2007; Jennings et al. 2017), and predation risk (Hammerstein and Riechert 1988; Jakobsson et al. 1995; Brick 1998). The results of this study further contribute to our understanding of these costs. For example, studies that have previously quantified the energetic costs of combat frequently quantified the costs associated with physical activity (e.g., the amount of energy it takes a cricket to charge at their opponent; Hack 1997). However, our study reveals that physical activity is not the only factor that can contribute to the energetic costs of combat.

Our finding that an acute injury has an energetic cost is not surprising (Lochmiller and Deerenberg 2000; Ardia et al. 2012). However, the observed effect size was limited (an approximately 3% increase in an individual's RMR), especially given the large size of the puncture wounds. In other insects, for example, wounding can increase RMRs by 28% (Ardia et al. 2012). Moreover, when birds are presented with an immune challenge, their RMR increases from 5 to 15% (Hasselquist and Nilsson 2012). The metabolic costs measured here may be low because fighting-related damage in coreids mainly occurs more-or-less peripherally on the wings (specifically the corium; Emberts and Wiens 2021), as opposed to the main body. Moreover, given that approximately half of the males sampled from a population have wing punctures (i.e.,

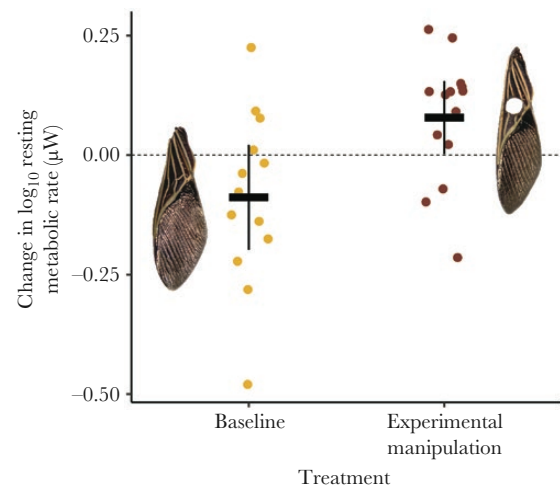


Figure 2

Simulated fighting injuries increase an individual's resting metabolic rate (RMR). The RMR of experimentally damaged individuals increased, whereas the RMR of non-injured individuals (i.e., baseline) slightly decreased. The dashed line indicates where an individual (i.e., a datapoint) would be if they had the exact same resting metabolic rate both before and after they received their treatment. Rectangles indicate a treatment's mean value, whereas error bars visualize 95% confidence intervals. Note that the 95% confidence intervals for our baseline treatment include zero, whereas the 95% confidence intervals for our experimental manipulation treatment exclude zero. Wing photographs adjacent to each rectangle visually depict the damage treatments (no damage or 3 mm punctures).

We thank Cody Howard for his help with data collection. We also thank the anonymous reviewers for providing helpful feedback on an earlier version of the manuscript.

Data availability: Analyses reported in this article can be reproduced using the data provided by Emberts, Somjee, et al. (2021)).

Handling editor: Mark Briffa

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