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Weapon performance drives weapon evolution

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Many sexually selected traits function as weapons, and these weapons can be incredibly diverse. However, the factors underlying weapon diversity among species remain poorly understood, and a fundamental hypothesis to explain this diversity remains untested. Although weapons can serve multiple functions, an undeniably important function is their role in fights. Thus, a crucial hypothesis is that weapon diversification is driven by the evolution of weapon modifications that provide an advantage in combat (e.g. causing more damage). Here, we test this fighting-advantage hypothesis using data from 17 species of coreid bugs. We utilize the fact that male–male combat in coreids often results in detectable damage, allowing us to link different weapon morphologies to different levels of damage among species. We find that certain weapon morphologies inflict much more damage than others, strongly supporting the fighting-advantage hypothesis. Moreover, very different weapon morphologies can inflict similarly severe amounts of damage, leading to a weapon performance landscape with multiple performance peaks. This multi-peak pattern could potentially drive different lineages towards divergent weapon forms, further increasing weapon diversity among species. Overall, our results may help explain how sexually selected weapons have evolved into the diversity of forms seen today.

1. Introduction

Sexual selection has led to the evolution of some of the most bizarre and elaborate traits seen in animals [1], and based on some estimates, almost half (approx. 44%) of these traits are used in contests between males [2]. Contest-related traits include numerous types of weapons, such as the branching antlers of deer, the enlarged claws of fiddler crabs and the elongated horns of rhinoceros beetles [3,4]. These sexually selected weapons may represent up to a third of an individual's body mass (e.g. claws in fiddler crabs [5]) and can be more than twice an individual's body length (e.g. front legs in harlequin beetles [6]). Moreover, these weapons can differ dramatically in their size and shape among closely related species [3]. For example, among species of dung beetles, horns can resemble crowbars, tridents and spears [7]. Yet, the evolutionary mechanisms that underlie the diversification of these weapons among species remain unclear.

Several hypotheses have been proposed to explain the diversity of weapon shapes among species [8]. One of the most well-supported hypotheses proposes that weapon diversification results from differences in how and/or where the weapons are used, called the divergent-context hypothesis [3,9,10]. For example, bovids that wrestle with their opponents are more likely to have horns with long central arches [9]. A similar association between fighting behaviour and weapon shape has been observed in rhinoceros beetles as well [11].

The divergent-context hypothesis is demonstrably important, but another straightforward hypothesis about weapon evolution has yet to be tested. Although weapons can potentially have many functions [3,8], they are primarily used to fight [8]. Thus, a crucial but still untested hypothesis is that weapon diversification is driven by selection for weapon modifications that provide an

Figure 1. Weapons and wing damage in the coreid bug *Acanthocephala femorata*. Male *A. femorata* (pictured) use their enlarged, spined hind legs to compete with other males over access to females and resources [20]. In this species, there are prominent spines on the inner surface of the femora. When these competitions escalate, there can be severe damage to the forewings (figure 2). In the individual shown, there are notable punctures on the left forewing. (Online version in colour.)

advantage in combat (i.e. the fighting-advantage hypothesis [8]). There are several ways that weapon modifications could provide a fighting advantage. For weapons that inflict injuries during fights, both theoretical [12–17] and empirical evidence [18,19] suggests that damage can have an important role in determining the contest winner. Thus, one way a fighting advantage could manifest itself is through an increase in the amount of damage that a weapon causes.

Here, we use data from coreid insects (Hemiptera: Coreidae) to test the fighting-advantage hypothesis for the first time. Coreids offer an excellent system to test this hypothesis. First, in contrast with most other systems, the frequency and severity of injury from male–male combat can readily be quantified (figures 1 and 2), as explained below. Moreover, experimental manipulations have demonstrated that this damage can influence fighting outcomes [19]. Second, there is considerable diversity in weapon form across the clade (figure 3), and similar weapons have evolved repeatedly across the group, providing statistical power for comparative analyses [21]. This weapon diversity involves variation in the morphology of their enlarged hind legs (e.g. femur size, number of spines), which are used in male–male competition over access to females and territories [20,22–26]. Despite the diversity of weapon forms, coreid weapons are used in a behaviourally similar manner—to squeeze their opponents [20,22–26].

When coreids use their weapons to squeeze their rivals, the rival's wings can become damaged (figures 1 and 2) [23]. Damage in this context is permanent because adult coreids are in their terminal moults and hemimetabolous insects cannot regenerate without moulting [27,28]. This damage also appears costly. The melanization that is often observed around the puncture wounds (figure 2) is indicative of an immune response, which can be metabolically expensive [29,30]. Moreover, wing damage has been shown to reduce flying ability in insects [31,32]. Thus, the wing damage observed here may have implications for an individual's ability to find mates, forage and evade predators. Such costs probably explain why wing damage can influence fighting outcomes in this clade [19].

The fighting-advantage hypothesis leads to clear macro-evolutionary predictions in coreids. One way that a weapon

modification may provide a fighting advantage is by increasing the amount of damage that the weapon can induce [12–19]. Therefore, this hypothesis would be supported if there is a positive relationship between particular weapon modifications (e.g. additional spines, increased femur width) and the severity of damage inflicted on conspecifics by these weapons. We tested this hypothesis by quantifying weapon diversity and damage from male–male competition among 17 coreid species. We then used phylogenetic generalized least-squares (PGLS) regressions [33] to determine whether weapon modifications (e.g. spines, femur width) were positively associated with damage severity.

2. Methods

(a) Sampling

We selected 17 coreid species to include based on: (i) their presence in a time-calibrated, multi-locus phylogeny for the family; (ii) the presence of male–male competition in these species; and (iii) their representation of the diverse weapon morphologies that occur in coreids. The phylogeny reported by Emberts *et al.* [21] included 47 coreid species. Among these 47 species, 18 have non-weaponized hind legs (hind legs that resemble their middle legs) and 29 have weaponized hind legs (hind legs that were enlarged and had spines). Among these 29 species, there is published evidence that weaponized hind legs are used in male–male combat in the following species: *Acanthocephala declivis* [23], *Ac. femorata* [20], *Mictis profana* [25], *M. longicornis* [34], *Leptoscelis tricolor* [24], *Narnia femorata* [26] and *Leptoglossus gonagra* (synonymous with *Leptoglossus australis* [22]). Moreover, our previous work [21] revealed several other species that had wing damage that was characteristic of male–male competition. Therefore, these species were included as well (*Acanthocephala terminalis*, *Anoplocnemis phasiana*, *An. curvipes*, *Phthiacnemia picta*, *Physomerus grossipes*, *Piezogaster calcarator* and *Thasus neocalifornicus*). Finally, we wanted to ensure that the diversity of weapon forms across the 47 phylogenetically sampled species was represented. Therefore, we also included *Euthochtha galeator*, *Merocoris typhaeus* and *Zicca taeniola*. Their unique weapon morphologies are apparent in figure 3 (numbers 8–10).

We did not include species with non-weaponized hind legs in our study because doing so could bias the results. Specifically, since species with non-weaponized legs should have no damage from these weapons, we predicted that including species without weapons would only strengthen the observed relationships between damage and weapon morphology. We performed analyses after adding in 11 species with non-weaponized legs and found that the relationship reported in the main text (see below) indeed became stronger (electronic supplementary material, appendix S1). Thus, excluding species with non-weaponized legs is a more conservative approach.

For most species, the specimens used were collected by us and were all sampled from a single locality per species (electronic supplementary material, table S1), to avoid potentially confounding effects of within-species geographic variation on the analyses. However, museum specimens and specimens collected by colleagues [21] were also used to include four additional species. For three of these species (*Anoplocnemis phasiana*, *Physomerus grossipes* and *Mictis longicornis*), most specimens were from the small island of Singapore (total area = 722 km^2), although some were from neighbouring countries. Additionally, sampled specimens of *Anoplocnemis curvipes* were from across southeastern Africa. We used an ANOVA to confirm that these four species had a similar standard deviation in body size as the other 13 species ($F_{1,15} = 0.065$, $p = 0.802$), which were each collected from a single location.
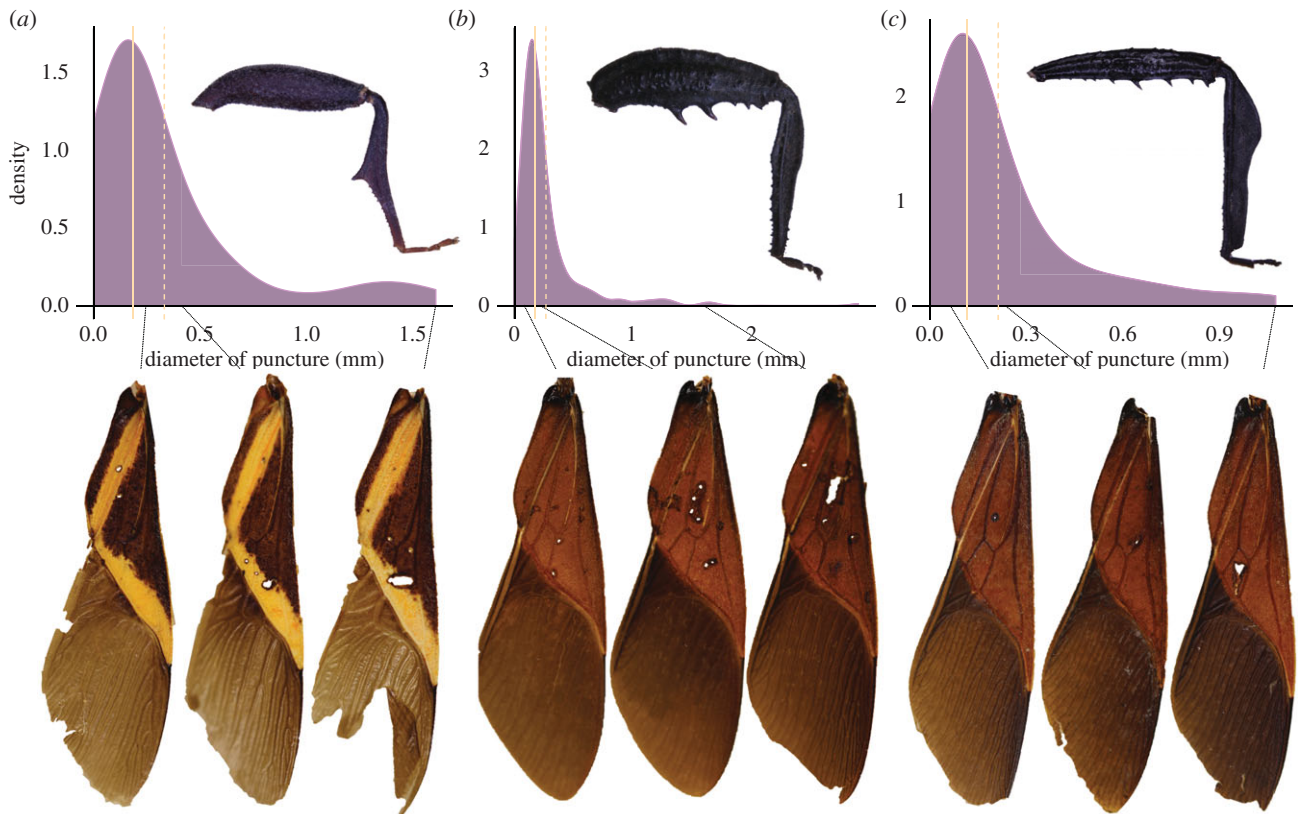
Figure 2. The severity of injury from male–male competition in three species of coreid bugs. The density plots show the distribution of damage severity (maximum diameter of a puncture) to the forewings across all measured individuals of (a) *Mictis profana* (*n* = 47 punctures), (b) *Acanthocephala femorata* (*n* = 254 punctures) and (c) *A. declivis* (*n* = 60 punctures). Dashed tan lines represent mean puncture size and solid tan lines represent median puncture size. For reference, the largest puncture wounds in each of the pictured forewings (from left to right) are (a) 0.202, 0.461 and 1.607, (b) 0.088, 0.202 and 1.606, and (c) 0.077, 0.235 and 1.075 mm. All wing pictures were modified (backgrounds removed) to help visualize puncture wounds. A photographed example of each species's hindlimb weapon (in lateral view) is shown above the distributions. (Online version in colour.)

To quantify the damage from male–male competition, we measured an average of 41.1 males per species (mean = 41.1, median = 32, range = 11–104; electronic supplementary material, table S1). We then measured up to 20 males per species to quantify weapon morphology (mean = 15.2, median = 16, range = 5–20; electronic supplementary material, table S1). Importantly, individuals measured for weapon morphology included both specimens that had wing damage and those that did not. We specifically measured a random subset of the specimens' right hind leg weapons. Only right hind legs were measured given high levels of symmetry between right and left legs [35].

(b) Data collection

To quantify weapon form in coreids, we measured seven hind leg weapon components from each specimen when possible. All linear measurements were taken to the nearest micrometre in ImageJ (version 1.46 [36]) from photographed individuals.

We specifically measured: (i) maximum femur width; (ii) femur length; (iii) tibial length; (iv) length of the longest spine; (v) the location of the longest spine; (vi) distance from the longest spine to the fulcrum; and (vii) the number of prominent spines on the right hind leg (electronic supplementary material, figure S1). The femur width measurement captured the widest portion of the femur and did not include spines. If the widest part of the femur had a spine, the measurement only extended to the spine's base. Femur length was the distance between the trochanter–femur joint and the femur–tibia joint. The tibial length was the distance between the femur–tibia joint and the tibia–tarsus joint. Spine length was the distance between the base and the tip of the longest spine. Location of the longest spine was the distance between the middle of the longest spine's

base and the trochanter–femur joint (i.e. the fulcrum). Spines that were distal to the trochanter–femur joint (on the tibia) were treated as negative values for location. Spines that were proximal to the trochanter–femur joint (on the femur) were treated as positive values. The absolute values of the spine location measurements were then used as the distance between the fulcrum and the longest spine. To determine the number of prominent spines, the number of spines that were greater than or equal to approximately half the length of the longest spine were counted. Pronotal width, a proxy for body size in this group [21,37], was also measured. This proxy allowed morphological measurements to be size corrected. The final values used for each species were mean measurements among specimens (electronic supplementary material, table S1).

Tibial flags (a tibial dilation found in some coreids) were not considered weapons for two main reasons. First, tibial flags are thought to instead have a role in predator–prey interactions [38]. Second, there can be extreme sexual dimorphism in tibial flag size, but not in the pattern expected for a trait involved in male–male combat. For example, female *Acanthocephala femorata* have large tibial flags, but tibial flags in males are practically absent [38].

To assess wing damage from male–male competition, we quantified three aspects of damage: (i) the proportion of individuals per species with one or more wing punctures; (ii) the median number of punctures per damaged individual; and (iii) the median size of the punctures in each species. Size measurements were taken to the nearest micrometre in ImageJ from photographed individuals. Each species's median puncture size was calculated using all puncture measurements (electronic supplementary material, tables S1). The median results were prioritized over the mean because visualizations of
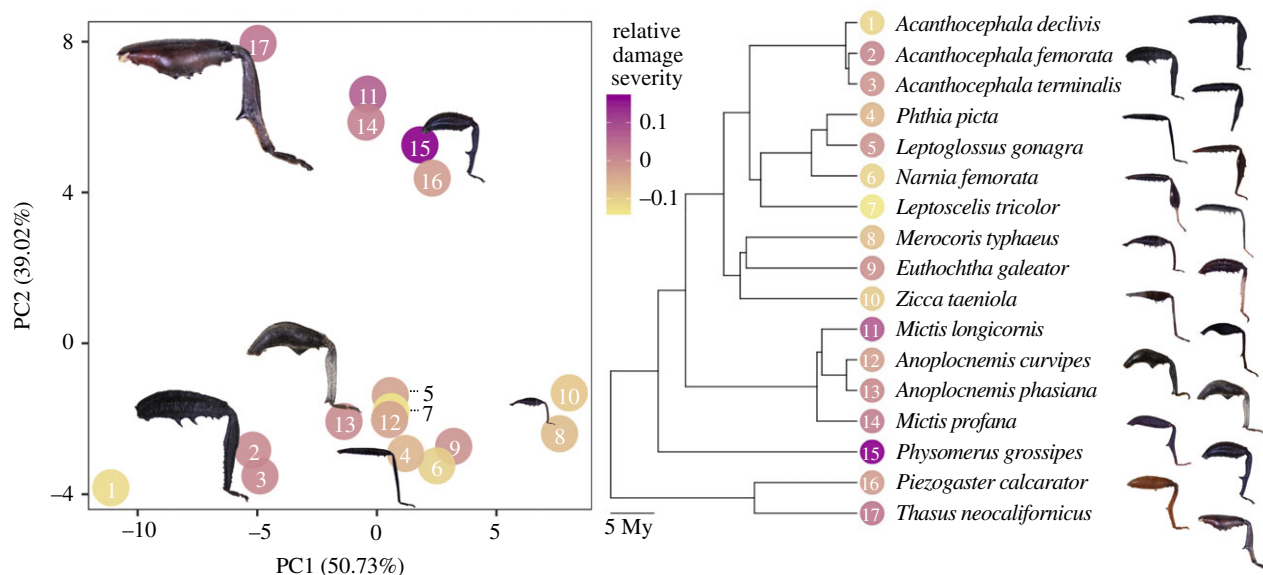
Figure 3. Weapon diversity, damage severity and phylogeny among 17 species of coreid bugs. Weapon diversity was quantified using a phylogenetic principal component analysis. The first two principal components (PCs) explained 90% of the variation in the data (electronic supplementary material, table S4). PC1 reflects size. PC2 reflects variation in weapon shape. For example, weapons of *Thasus neocalifornicus* (no. 17) and *Acanthocephala femorata* (no. 2) have highly negative PC1 scores because they are large (in terms of absolute size). However, *T. neocalifornicus* has a higher PC2 score than *A. femorata* because it has a wider femur, fewer prominent spines, and the longest spine is halfway down the tibia. As PC2 increases so does relative damage severity (figure 4). The six selected hind leg images capture most of the observed diversity in weapon size and shape (from species 2, 4, 8, 13, 15, 17 in the tree; the image contacts the corresponding species number). Colour corresponds to relative damage severity, with purple being more severe and tan being less. Numbers on the graph correspond with numbers on the phylogeny. The phylogeny is time-calibrated, and the scale bar indicates the branch length associated with 5 million years. A photographed example of each species weapon is provided directly across from each species tip so that variation in weapon shape can more easily be visualized. (Online version in colour.)

the damage data often revealed a right-skewed distribution, making the median a better measure of central tendency (figure 2). However, both measures of central tendency produced similar results (see results and electronic supplementary material, tables S2 and S3). Wing punctures were the focus of this study because wing frays and tears may be due to predation or usage [39].

(c) Statistical analyses

We used two complementary approaches to quantify weapon form in coreids. First, we quantified the diversity of weapon shapes with a phylogenetic principal component analysis (pPCA [40]). The pPCA was carried out in R (version 3.6.0 [41]) using the package *phytools* (version 0.6–60 [42]). The pPCA included all seven weapon components. We then used the scree plot method to determine the number of PCs to retain [43]. We predicted that PC1 would reflect size, and additional PCs would reflect weapon shape.

Second, we analysed each weapon component individually. We size corrected each weapon component by first conducting PGLS regression with the R package *caper* version 1.0.1 [44]. All PGLS analyses used the lambda value estimated with maximum-likelihood. For each weapon component, we conducted a PGLS analysis including pronotal width (a body size proxy) as the independent variable and each weapon component as the dependent variable. We then extracted the residuals from each of these models. These residuals were then used as the size-corrected shape for each weapon component. Because we tested multiple traits for this second analysis, we applied a sequential Bonferroni correction to each table of these results [45].

We then conducted PGLS analyses to test whether weapon modifications provide an advantage in combat (fighting-advantage hypothesis). One obvious way that weapon modifications may provide an advantage in combat is by increasing the amount of damage induced. Therefore, we investigated how our

three damage metrics were related to each of the seven size-corrected weapon components and to composite weapon shape (PC2). We size-corrected maximum puncture width as described for weapon components. Size correcting puncture width was important because a puncture wound with a diameter of 0.2 mm should have greater fitness costs for a smaller individual than a larger one (a higher percentage of the wing missing).

Given that this is one of the first studies to quantify the damage from male–male competition among species, we also investigated whether the frequency of damage observed among species was associated with: (i) absolute weapon size (PC1), (ii) intraspecific variation in femur width or (iii) intraspecific variation in pronotal width. We specifically investigated whether absolute weapon size was associated with the frequency of damage because it has previously been proposed that the most enlarged and elaborated weapons among species rarely inflict damage [3], and our data allowed us to test this hypothesis. Previous studies have also found that coreid fights are more likely to occur when rivals are similar in size [46]. Thus, we wanted to know whether species that had more similar body sizes or femur sizes among sampled individuals (i.e. lower standard deviations for these traits) were more likely to have damage, potentially reflecting an increase in the frequency of damage-inducing fights.

For all comparative analyses, we used a recent time-calibrated phylogeny of Coreidae [21]. This phylogeny was estimated using a maximum-likelihood analysis of 567 loci. The tree was then dated using penalized likelihood [47] and four fossil calibration points. The phylogeny had very strong bootstrap support (all nodes with bootstrap values ≥90%). Therefore, performing comparative analyses across a distribution of trees from these data to address topological uncertainty should yield identical results (but no such distribution was available from these likelihood analyses). This 62-species phylogeny was then pruned to include only the 17 coreid species sampled here. All phylogenies, code, and other data are available on Dryad (see 'Data accessibility' below).
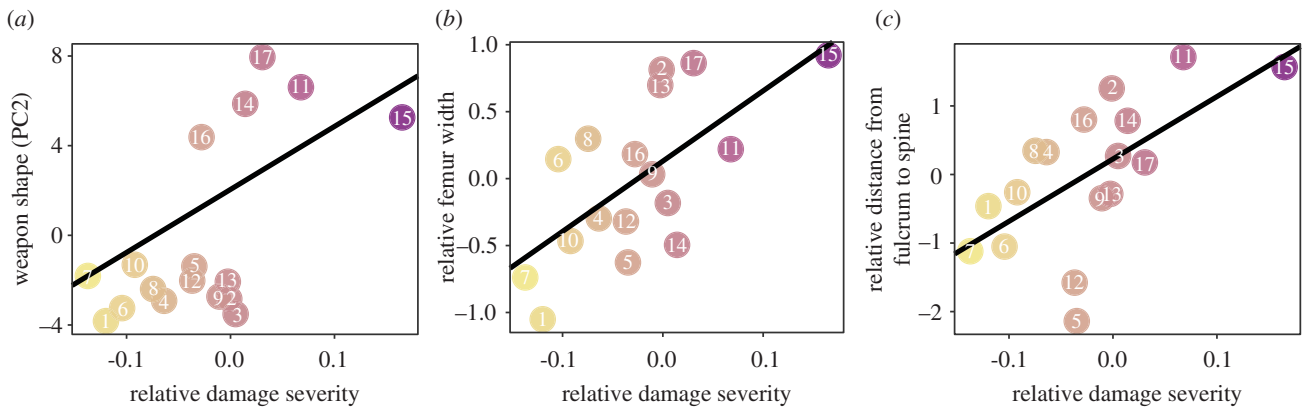
Figure 4. Weapon modifications are positively related to damage severity among coreid species. (a) PC2 (weapon shape metric) increases with relative damage severity ($t = 2.666$, $p = 0.018$, $r^2 = 0.322$). Both femur width and the distance between the longest spine and the fulcrum strongly load onto PC2 (electronic supplementary material, table S4). When we analyse femur width (b) and distance from the longest spine to the fulcrum (c) as individual weapon components, both traits increase with relative damage severity (femur width: $t = 3.356$, $p = 0.004$, $r^2 = 0.429$; distance from the longest spine to the fulcrum: $t = 3.131$, $p = 0.007$, $r^2 = 0.395$). Regression lines are based on PGLS, but the raw size-corrected data are shown here for ease of interpretation. Numbers in data points correspond with numbers in figure 3. (Online version in colour.)

3. Results

To quantify the diversity of weapon forms among the sampled coreid species, we conducted a pPCA with seven weapon components (electronic supplementary material, table S1). The scree plot revealed an obvious break in eigenvalues between the second and third PCs (electronic supplementary material, figure S2). Thus, we focused on the first two PCs here. PC1 explained 50.73% of the variance. Most variables related to weapon size loaded strongly onto PC1 (figure 3; electronic supplementary material, table S4). PC2 explained 39.02% of the variance. Femur width, number of prominent spines and two measures of location of the longest spine all loaded strongly on PC2 (electronic supplementary material, table S4). Since PC2 included most variation in weapon morphology that is uncorrelated with size (PC1), we refer to PC2 as weapon shape.

To quantify forewing damage in each species, we measured: (i) the proportion of individuals that had at least one wing puncture; (ii) the median number of punctures per damaged individual; and (iii) the median size of punctures. We observed punctured wings in 13 of the 17 sampled species. The four species without damage were *Leptoscelis tricolor*, *Merocoris typhaeus*, *Narnia femorata* and *Zicca taeniola*. Thus, none (0%) of the sampled individuals in these species had punctured wings. Our main results are consistent whether or not we included (see below) or excluded (electronic supplementary material, tables S5–S6) these four species from our analyses. For species with one or more punctures observed, the proportion of injured individuals ranged from 5 to 50%. The size of puncture wounds also varied among species. The largest were in *Physomerus grossipes* (median width = 0.295 mm), and the smallest in *Phthiacnemia picta* (median width = 0.044 mm; electronic supplementary material, table S1). *Physomerus grossipes* also had the fewest punctures per damaged individual (median puncture number = 1) and one of the lowest proportions of damaged individuals (12%; electronic supplementary material, table S1), suggesting these two measures may be negatively related with puncture size. However, phylogenetic (PGLS) regressions showed that neither median puncture number ($t = 0.806$, $p = 0.433$, $r^2 = 0.042$) nor proportion of injured individuals ($t = -0.836$, $p = 0.416$, $r^2 = 0.045$) were significantly related to relative puncture size across all species.

However, median puncture number and the proportion of damaged individuals were positively related ($t = 3.594$, $p = 0.003$, $r^2 = 0.463$).

The main focus of our study was to determine whether weapon modifications were positively related to damage severity, which would support the fighting-advantage hypothesis. Thus, we first investigated whether weapon shape (PC2) was associated with our three damage measures using PGLS regressions. We found that weapon shape (PC2) was positively related to relative puncture size ($t = 2.666$, $p = 0.018$, $r^2 = 0.322$; figure 4). However, weapon shape (PC2) was not significantly related to the median number of punctures per damaged individual ($t = 0.080$, $p = 0.937$, $r^2 < 0.001$) nor the proportion of injured individuals ($t = -0.716$, $p = 0.485$, $r^2 = 0.033$). Thus, weapon shape was associated with an increase in puncture size, but not the frequency with which punctures occurred. Analysing each weapon component individually revealed comparable results (table 1; electronic supplementary material, tables S7–S8). For example, we found that relative puncture size increased with both femur width and the distance between the longest spine and the fulcrum (figure 4).

We also tested whether the amount of intraspecific variation in pronotal width, intraspecific variation in femur width or absolute weapon size were associated with the frequency of damage observed among species. We found that damage frequency was positively associated with intraspecific variation in both pronotal width ($t = 2.681$, $p = 0.017$, $r^2 = 0.324$) and femur width ($t = 4.670$, $p < 0.001$, $r^2 = 0.593$). Thus, species with adult males that were more dissimilar in size (i.e. higher standard deviations) were more likely to have damage from fighting, the opposite of our prediction. We also found that the proportion of damaged individuals increased as absolute weapon size increased (PC1; $t = -3.343$, $p = 0.004$, $r^2 = 0.427$).

4. Discussion

Sexually selected weapons show a bewildering diversity of shapes across many animal groups, but the mechanisms underlying this diversity remain incompletely understood. Here, we tested the fighting-advantage hypothesis [8] as an explanation

Table 1. Results of PGLS regressions between weapon components (dependent variables) and median damage severity (independent variable). Italics indicate significant results after applying a sequential Bonferroni correction. Results using mean damage severity are given in electronic supplementary material, table S3.

weapon component	t	p	r²
femur width	*3.356*	*0.004*	*0.429*
femur length	−0.095	0.926	0.001
distant from longest spine to fulcrum	*3.131*	*0.007*	*0.395*
spine location	−2.058	0.057	0.220
spine length	0.670	0.513	0.029
tibial length	0.332	0.744	0.007
number of prominent spines	*−3.111*	*0.007*	*0.392*

Figure 5. A weapon performance landscape for coreids. This figure is a revisualization of figure 3, but in three-dimensional space. The vertical axis shows the amount of damage that the weapon inflicts in each species (relative damage severity: a size-corrected measure of median puncture size), a measure of weapon performance. The horizontal plane is weapon diversity on two PC axes. This visualization of the data shows that there are at least two performance optima (which can also be visualized in a contour plot; electronic supplementary material, figure S3). One performance optimum is associated with species that have their longest spine on the femur (e.g. illustrated here with *Acanthocephala femorata*, no. 2). The second optimum is associated with species that have their longest spine on the tibia (e.g. *Mictis profana*, no. 14). Selection on weapons to be more effective should generally drive lineages towards their closest performance peak. The two species shown illustrate that two different weapon morphologies can inflict almost identical amounts of damage. Numbers in data points correspond with numbers in figure 3. (Online version in colour.)

for this diversity. Based on an analysis of 17 coreid species, we found that certain weapon morphologies (e.g. relatively wide femurs) inflict more severe damage than others. Both theoretical [12–17] and empirical evidence [18,19] suggests that damage can have an important role in determining the contest winner. Thus, our results support the fighting-advantage hypothesis. This hypothesis may explain much of the weapon diversity seen in animals because most sexually selected weapons have a crucial role in fights [3,4,8].

The support for the fighting-advantage hypothesis found here suggests that there is selection for weapon modifications (e.g. a wider femur) that provide an advantage in combat. If there is indeed selection to improve weapon performance, then why have all coreid weapons not evolved to look the same? The diversity of weapon shapes observed in coreids may simply reflect the fact that species are evolving towards a weapon shape that optimizes their performance, and that some species are closer than others to reaching it. Alternatively, conflicting selective pressures may be inhibiting species from reaching their weapon performance optimum, further contributing to the maintenance of weapon diversity in this clade.

Several hypotheses have been proposed to explain weapon diversification [8], and these hypotheses are not mutually exclusive. As a result, multiple hypotheses may help explain weapon diversity within a clade. For example, one reason that *Mictis profana* may have a narrower femur than *Physomerus grossipes* is because of selection to reduce the cost of weaponry in *M. profana* (i.e. divergent cost hypothesis [48]). In coreids, weapon investment comes at the expense of testes investment [49–51]. Therefore, if testes are more important for reproductive success in *M. profana* than *P. grossipes*, then selection to reduce the cost of weaponry (to increase investment in testes) could potentially explain why *M. profana* have narrower femurs. A similar argument could be made for the divergent-context hypothesis (via difference in fighting behaviours). Previous studies on coreid fighting behaviour have all found that coreids use their weapons to squeeze their rivals [20,22–26]. However, in addition to using their weapons to squeeze, at least one coreid species (i.e. *Narnia femorata*) also uses their weapons to kick their rivals [46]. Thus, species that exclusively rely on their hind leg weapons for squeezing may require relatively wide femurs (with larger squeezing muscles
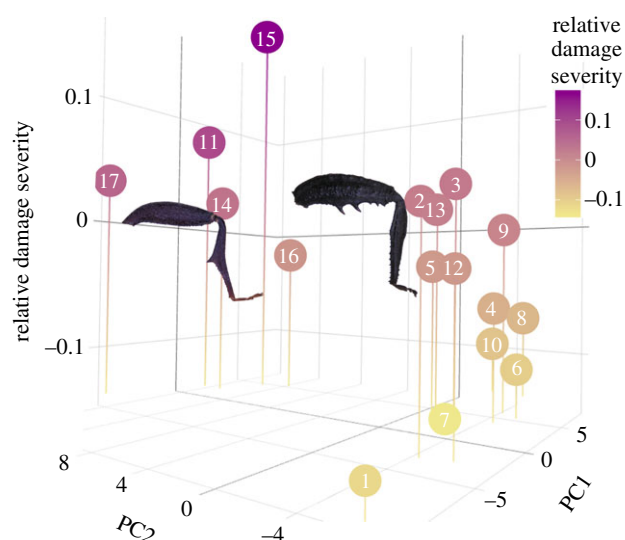
[52,53]; for a biomechanical explanation of the results, see electronic supplementary material, appendix S2). By contrast, species that squeeze *and* kick (e.g. *Narnia femorata*) may be able to win some fights with kicks alone (but see [46]). As a result, species that kick and squeeze may have relaxed selection on femur width.

Another way that weapon diversity can arise is if different weapon forms yield similar performance outcomes (i.e. many-to-one mapping of form to function [54–56]). This can be conceptualized through a framework similar to that of an adaptive landscape [57]. In this case, weapon performance is on the vertical axis, while the weapon form is on the horizontal plane (figure 5). If this landscape has multiple performance peaks, then selection on morphological traits to be more effective can drive different clades towards different optima. Simulations have shown that this overall process can increase morphological diversity [54]. In coreids, for example, both *Physomerus grossipes* and *Acanthocephala terminalis* inflict severe damage (figure 5). However, their weapon forms differ: *P. grossipes* has its longest spine on its tibia and *A. terminalis* has its longest spine on its femur. Thus, coreids can successfully inflict damage onto their opponents' wings if their prominent spine is on either their femur *or* tibia (i.e. the ability to inflict wing damage is not dependent upon the location of the longest spine). This pattern suggests that the weapon performance landscape in coreids has multiple optima (figure 5). It should be noted that other

factors besides weapon morphology (e.g. behaviour) probably contribute to this multi-optima pattern as well.

Overall, we found that much of the weapon diversity in coreids may be explained by the presence of multiple performance peaks and by species that have (for various reasons) failed to reach those peaks. Failure to reach a weapon performance peak may simply reflect the fact that a species is evolving towards its performance optima, but has yet to reach it. However, other hypotheses could also be invoked to explain why some species have not reached these peaks. Thus, future work should continue to investigate other hypotheses for weapon diversification in this clade, in addition to the fighting-advantage hypothesis.

Our study also challenges the idea that damage from male–male competition is uncommon in species with extravagant weaponry [3]. For example, in 6 of the 17 sampled weapon-bearing species, more than 20% of measured males had damage (electronic supplementary material, table S1). Moreover, larger weapons were associated with more frequent damage. Our study is not the first to document a high frequency of combat damage in species with elaborate weapons. Intraspecific competition in porcelain crabs [58] and intrasexual competition in Japanese horned beetles [59] also frequently result in substantial injury. In both species, approximately 40% of sampled fighting individuals had fracture wounds [58,59]. At such a high frequency, combat damage could have many additional evolutionary consequences beyond weapon morphology. For example, combat damage might influence the evolution of immune systems and/or promote the evolution of damage-reducing structures [19].

Our results also show that the frequency of damage from male–male competition can vary dramatically, even among closely related species. For example, just within the genus *Acanthocephala* the frequency of damage among species ranged from 18% to 50% of sampled individuals per species (electronic supplementary material, table S1). Given the potential implications of damage from male–male competition, future work should consider factors that might be responsible for this variation. It is possible that species with higher frequencies of damage have less variation in body size or weapon size and are thus more likely to escalate to high intensity (i.e. damage inducing) interactions. However, we found no evidence to support this hypothesis here, as species with less variation in size (i.e. species that had lower standard deviations) were less likely to have damage, not more. Furthermore, survivor biases might have biased perceptions of the frequency and severity of injury, both in this study and others. We quantified damage by looking at individuals that were collected from the wild and were alive when collected. As a result, we actually quantified the frequency and severity of damage from male–male competition that does not result

in death. Death from male–male competition is documented in at least one coreid species (*Acanthocephala femorata* [20]). This could mean that we underestimated the true frequency and severity of damage. If this is true, the consequences of damage could be even more pronounced. Another potential issue with using wild-caught coreids is that we were unable to age the specimens (beyond being an adult). Thus, we could not verify whether specimen ages were similar across the sampled species. Different distributions of ages for different species could potentially obfuscate the results because older specimens would have had more time to accumulate damage. This could be one reason why we did not find a significant association between weapon shape and the median number of punctures per species. Nevertheless, despite these potential sources of error, we were still able to recover strong relationships between damage severity and weapon morphology.

In summary, we show that much of the weapon diversity in coreids can be explained by how well different weapon morphologies perform at inflicting damage. To our knowledge, this study is the first to show how weapon performance (i.e. at inflicting damage) is related to weapon evolution and diversity among species. We also show that a weapon performance landscape can have multiple performance peaks (figure 5). Thus, selection to win fights could also be driving different lineages towards divergent weapon forms (i.e. many-to-one mapping of form to function), further contributing to overall weapon diversity among species. Finally, in addition to supporting a fundamental hypothesis about the causes of weapon diversity, we show that extravagant weapons can frequently inflict damage (and that larger weapons seem to inflict damage more often). Thus, our results and those of others (e.g. [59]) suggest that damage from male–male combat might be more widespread than previously considered [3].

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