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Do sexually selected weapons drive diversification?

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Sexual selection is often thought to promote speciation. This expectation is largely driven by the fact that sexually selected traits can influence mating patterns and contribute to reproductive isolation. Indeed, some comparative studies have shown that clades with sexually selected traits have increased rates of speciation and diversification. However, these studies have almost exclusively focused on one mechanism of sexual selection: female choice. Another widespread mechanism is male-male competition. Few empirical studies (if any) have investigated the role of this alternative mechanism in driving diversification. Nevertheless, recent reviews have suggested that male-male competition can increase speciation rates. Here, we investigated whether traits associated with precopulatory male–male competition (i.e., sexually selected weapons) have promoted speciation and diversification in insects. We focused on three clades with both weapons and suitable phylogenies: leaf-footed and broad-headed bugs (Coreidae+Alydidae; ∼2850 species), stick insects and relatives (Phasmatodea; ∼3284 species), and scarab beetles (Scarabaeoidea; ∼39,717 species). We found no evidence that weapon-bearing lineages in these clades have higher rates of speciation or diversification than their weaponless relatives. Thus, our results suggest that precopulatory male-male competition may not have strong, general effects on speciation and diversification in insects, a group encompassing ∼60% of all described species.

KEY WORDS: Diversification, female choice, insects, male-male competition, sexual selection, speciation, weapons.

A major aim of evolutionary biology is to explain the uneven distribution of species richness across branches on the Tree of Life. For example, among animal phyla, Arthropoda includes approximately 80% of all described animal species (with >1.2 million), whereas others (like Placozoa) contain fewer than five (Zhang 2013). What explains such dramatic differences in richness? Broad-scale analyses across life suggest that much of the variation in species richness among named clades of similar age (e.g., families, orders, phyla) is explained by variation in rates of diversification (Scholl and Wiens 2016). The diversification rate of a clade is the rate at which it accumulates species richness, or the rate of speciation minus the rate of extinction (Ricklefs 2007; Morlon 2014). Clades with high diversification rates can have high species richness despite being relatively young (like Arthropoda), whereas clades with low diversification rates may be relatively old but still have few species (like Placozoa). Several studies have now identified some traits that can help to explain differences in diversification rates among clades (reviewed in Wiens 2017). The types of traits that are generally the most important for explaining these patterns remains an open question (Wiens 2017). Another unresolved challenge is to relate studies of speciation among closely related species to large-scale patterns of diversification and richness.

Sexual selection is a key factor thought to promote speciation and net diversification (Panhuis et al. 2001; Ritchie 2007; Kraaijeveld et al. 2011). There is now an extensive body of work that shows how sexually selected traits (like songs and conspicuous coloration) can contribute to mating isolation and speciation among closely related species. However, it is less clear whether the impact of sexually selected traits on speciation can scale up to explain large-scale patterns of diversification and species richness. For example, there is strong evidence for the role of bird songs and frog calls in reproductive isolation and speciation among closely related species and populations (e.g., Hoskin et al. 2005; Boul et al. 2007; Wilkins et al. 2013; Uy et al. 2018), but no evidence that the presence of acoustic communication drives

large-scale patterns of diversification across terrestrial vertebrates (Chen and Wiens 2020). More broadly, evidence that sexually selected traits drive diversification is mixed (Panhuis et al. 2001; Ritchie 2007). Furthermore, the effect of sexual selection on diversification appears to be strongest at lower taxonomic scales (e.g., within families but not across orders; Panhuis et al. 2001; Kraaijeveld et al. 2011).

An important omission in much of the sexual selection literature is the potential role of male-male competition in speciation (reviewed in Qvarnström et al. 2012; Tinghitella et al. 2018). Male-male competition is a separate mechanism by which differential mating success can occur (Andersson 1994; McCullough et al. 2016), and it may be nearly as widespread as female choice (Wiens and Tuschhoff 2020). How exactly male-male competition promotes speciation is less clear, however. In sympatric stickleback species (*Gasterosteus aculeatus*), male-male competition between two lake-dwelling sympatric morphs (benthic, limnetic) is thought to generate disruptive selection against hybrid phenotypes, generating postzygotic reproductive isolation (Keagy et al. 2016). Another hypothesis is that ecological differences between allopatric populations could lead to divergence in traits related to male-male competition (Qvarnström et al. 2012; Tinghitella et al. 2018). For example, different signaling environments in allopatric populations (e.g., water clarity, open vs. shaded habitat) might favor different agonistic signals (Tinghitella et al. 2018). A third hypothesis involves agonistic interactions between males of different species in sympatry, leading to divergence in other traits to avoid competition (which might then drive reproductive isolation), such as asynchronous breeding times between closely related *Ficedula* flycatchers (Vallin et al. 2012). There is now support for some aspects of these different hypotheses in many empirical systems (reviewed in Tinghitella et al. 2018). At the same time, a reasonable criticism of some hypotheses is that it is not always clear how male-male competition would be the primary driver of reproductive isolation between incipient species, without invoking other processes (e.g., divergent female choice for divergent male phenotypes). Nevertheless, a clear macroevolutionary prediction is that if sexually selected traits associated with male-male competition do drive speciation, then species with these traits should have higher rates of speciation than those that do not (Tinghitella et al. 2018).

In addition to potentially increasing speciation rates, male-male competition may also provide some population-level benefits, which could result in reduced rates of extinction. However, the general relationship between sexual selection and extinction is unclear. Some studies have shown that sexual selection can reduce the effective population size, erode genetic variation, and limit the ability of populations to adapt to changing conditions (Kokko and Brooks 2003; Dugand et al. 2019). These could increase rates of extinction (Lande 1980; Tanaka 1996; Kokko and

Brooks 2003; Martinez-Ruiz and Knell 2017; Martins et al. 2018, Martins et al. 2020). On the other hand, theoretical and empirical work has also shown that sexual selection can remove deleterious alleles from the population, drive adaptive evolution, and ultimately protect against extinction (Lorch et al. 2003; Fricke and Arnqvist 2007; Long et al. 2012; Plesnar-Bielak et al. 2012; Matínez-Ruiz and Knell 2017; Parret and Knell 2018; Yun et al. 2018; Parrett et al. 2019; Cally et al. 2019). In summary, the presence of sexually selected traits associated with male-male competition could increase net diversification rates (speciation minus extinction), either by increasing the rate of speciation and/or decreasing the rate of extinction. However, to our knowledge, this prediction has yet to be empirically tested.

In this study, we use phylogenetic methods to test whether traits related to male-male competition influence diversification in the largest clade of animals: the insects. We specifically investigate whether the presence of sexually selected weapons (i.e., weapons used against rival males in combat over access to females) has promoted speciation and net diversification. These weapons are widespread in arthropods and chordates (Emlen 2008; Rico-Guevara and Hurme 2019) and can be relatively straightforward to assess, given their conspicuousness.

We focus on three insect clades: the bug clade Coreidae + Alydidae (Hemiptera), the beetle clade Scarabaeoidea (Coletoptera), and the order including the stick insects (Phasmatodea). These three clades were selected for three main reasons. First, sexually selected weapons have been documented within all three clades. Second, a time-calibrated phylogenetic tree including >50 species was available within each clade. Time calibration is essential for estimating diversification rates and a sampling of >50 species is thought to be crucial for state-dependent speciation-extinction models (see Methods). Third, the presence of weapons was variable within each clade, with multiple losses and/or gains (Fig. 1). This third criterion is especially useful for finding a statistical association between trait origins and increased diversification rates within clades. In addition to these three clades, we also considered other insect clades with weapons used in male-male competition, including wetas (Orthoptera), earwigs (Dermaptera), antlered flies (Diptera), and dobsonflies (Megaloptera). However, none of these clades met all three criteria.

Methods
TREES AND TRAIT DATA
Coreidae-Alydidae

We used the phylogeny of the sister families Coreidae and Alydidae reported in Emberts et al. (2020). This phylogeny includes ~2% of the extant species in this clade (59 out of 2850) and ~38% of the tribes (15 out of 40; Emberts et al. 2020). The
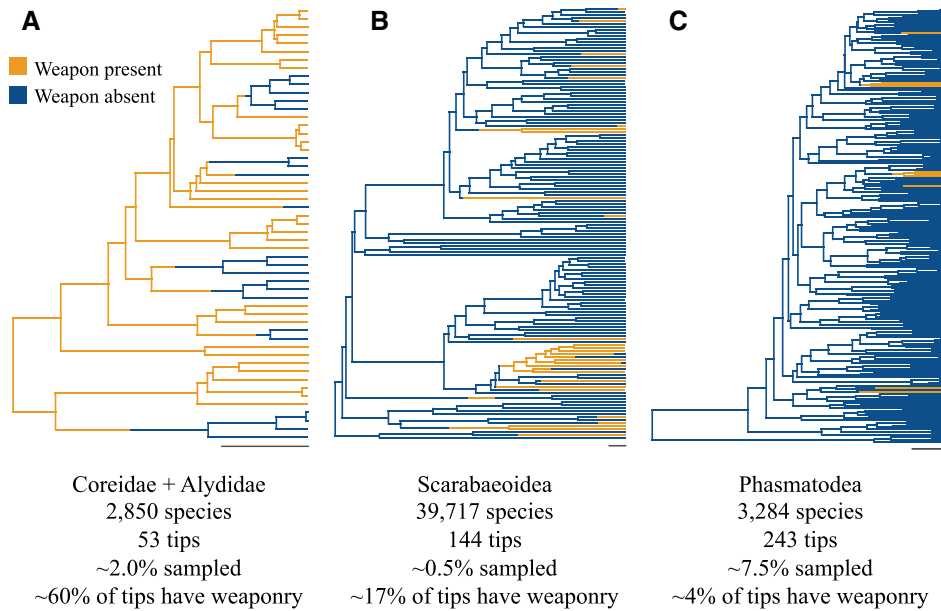
Figure 1. Phylogenies used to test the relationship between sexually selected weapons and diversification rates. Below the name of each group, we give the total number of described species in the clade (from Roskov et al. 2014), the number of species sampled in the tree (tips), the percentage of species sampled, and the percentage of sampled species that were scored as having weapons. For illustrative purposes only (not used in any analyses), we also show the evolution of sexually selected weaponry across the trees, in leaf-footed and broad-headed bugs (A), scarab beetles (B), and stick insects and relatives (C). Depicted is a stochastic character simulation (assuming equal rates) showing how sexually selected weaponry may have evolved in each clade, based on the observed states in the tips. These simulations were conducted with the R package *phytools* (version 0.6-60, Revell 2012) using the make.simmap function. Note that there are multiple transitions between states in all three clades. For the bug simulation (A), the ancestors is estimated to have a sexually selected weapon (i.e., the ancestral node is gold), with multiple losses of the trait. Conversely, the ancestor of phasmids (C) is estimated to be weaponless (i.e., the ancestral node is blue), with multiple origins of weaponry arising across the clade. Finally, the scarab beetle simulation (B) shows multiple gains and losses. These phylogenies are time calibrated, and the scale bar at the bottom of each phylogeny indicates the branch lengths associated with 10 million years.

59 species in this phylogeny represent almost all the species of Coreidae + Alydidae that those authors could acquire in Australia, Eswatini, Panama, Singapore, South Africa, and the United States (Emberts et al. 2020). This time-calibrated maximum likelihood phylogeny is based on 567 loci, and almost all nodes were strongly supported. Thus, there was little topological uncertainty, and no distribution of trees.

Emberts et al. (2020) also recorded whether 53 of the 59 species had males with enlarged hind femurs and hind leg spines. Male hind leg morphology for the remaining six species was not assessed because those authors only had female specimens for those six species. Males in many species in these families use their hind legs in competition over access to mates and territories, and all species that have been noted to do so share the same hind leg features (i.e., enlarged hind femurs and hind leg spines; Mitchell 1980; Miyatake 1993; Eberhard 1998; Miller and Emlen 2010; Okada et al. 2011; Tatarnic and Spence 2013; Emberts et al. 2018; Emberts and Wiens 2021). However, these morphological features will undoubtedly capture some species that do not engage in male-male competition (i.e., a false positive). For example, male *Leptoglossus phyllopus* have hind legs with enlarged femurs and spines. However, studies that have investigated the ecology of *L. phyllopus* have found no evidence that they engage in male-male combat (Mitchell 1980). As a result, we coded the presence of weaponry for this clade in one of two ways. First, we used the morphological coding of Emberts et al. (2020) and assigned all species with weapon-like morphology as having sexually selected weapons. Second, we only assigned a species as having a sexually selected weapon if there was published data documenting that the males use their weaponized hind legs in intrasexual combat (Mitchell 1980; Miyatake 1993; Eberhard 1998; Miller and Emlen 2010; Okada et al. 2011; Tatarnic and Spence 2013; Emberts et al. 2018; Emberts and Wiens 2021).

Scarabaeoidea

For Scarabaeoidea, we used the main tree reported in Ahrens et al. (2014; BEAST run 6). The 146 species of Scarabaeoidea used in this phylogeny were selected to represent all major

lineages and biogeographic regions (Ahrens et al. 2014). This tree included 0.5% of the extant species in this clade. We confirmed that there was a strong positive relationship between the number of species sampled per subclade (see below) and the number of describes species per subclade (t = 14.379, $P<0.001$, r^2 = 0.958, n = 11; Table S4). This strong relationship is the pattern expected if species are sampled randomly within the clade (an important assumption for some of our analyses, see below). We acknowledge that this strong relationship among subclades does not guarantee that sampling of species is fully proportional among all the higher taxa within each subclade. Nevertheless, if weapons do accelerate diversification, then species with weapons should be associated with shorter branch lengths on the tree (and this should be detected in a state-dependent speciation and extinction framework), even if sampling is not perfectly proportional at every level.

Ahrens et al. (2014) generated a single topology from their analyses, but they explored alternative divergence dates. Additional analyses confirmed that our results were similar regardless of which dated tree we used (see Results, Table S1).

Many species of Scarabaeoidea have horns, which are used in combat between males (e.g., Emlen et al. 2005, Emlen et al. 2007; Emlen 2008). To code the presence or absence of these weapons among the 146 sampled Scarabaeoidea species, we used data from the literature, digitized museum specimens, and photographs of museum-quality specimens. A recent study summarized the distribution of horns among major subclades of Scarabaeoidea (Ohde et al. 2018). They (Ohde et al. 2018) concluded that horns are absent in the following subclades: Trogidae, Sericini, Macrodactylini, Rhizotrogini, Melolonthini, Diplotaxini, Anomalini, and Adorentini. Thus, all the species in these subclades were treated as hornless. Moreover, species of Aphodiinae only have tiny horns (Ohde et al. 2018). These small protrusions seem unlikely to function in contests. Thus, species within this clade were coded as weaponless.

For other Scarabaeoidea species, we used photographs of male specimens to determine the presence or absence of horns. We initially coded a protrusion as a horn if the protrusion was larger than the individual's eye. We chose this approach for two reasons. First, it enhances replicability since horns and eyes are relatively close to one another and are often depicted in the same photos. Second, many beetle species have tiny protrusions that seem unlikely to function in male-male combat (e.g., some Aphodiinae) and we wanted to exclude these structures. However, horns which are only slightly larger than an individual's eye have been shown to be important in male-male competition (e.g., in small *Euoniticellus intermedius*; Pomfret and Knell 2006). We included these modestly sized weapons in our coding scheme, but this likely led to some false positives (i.e., species

identified as having a weapon when they do not). Therefore, we coded Scarabaeoidea horns in two ways: (1) species whose horns were similar in size to their eyes were considered to have weapons (a more liberal coding scheme), and (2) where these same species were not considered to have weapons (a more conservative scheme).

In addition to horns, sexually selected weapons in Scarabaeoidea also include exaggerated mandibles (e.g., Goyens et al. 2015) and legs (e.g., monkey beetles; Rink et al. 2019). A single species sampled here had sexually dimorphic legs, which we coded as a weapon (*Propomacrus bimucronatus*). Other species had horns.

If museum-quality photographs were unavailable for a given species, we randomly selected (via a random number generator) another species from the same genus for which there were museum-quality photographs. For two species of Scarabaeoidea (from 146), we could not find photographs or adequate literature descriptions of their morphology (i.e., adequate to determine whether weapons were present or not). These two species were excluded.

Finally, it is important to note that we treated all beetle horns as sexually selected weapons. We think this is reasonable because numerous studies have shown that Scarabaeoidea beetles with horns use these structures in competition over access to mates (e.g., Eberhard 1978; Siva-Jothy 1987; Cook 1990; Rasmussen 1994; Emlen 1997; Moczek and Emlen 2000). However, it is possible that some horns serve alternative functions. For example, *Mecynotarus tenuipes* in the beetle family Anthicidae (i.e., not in Scarabaeoidea) use their horns for digging, as opposed to fighting (Hashimoto and Hayashi 2012). We address the potential for coding errors in our analyses below.

Phasmoidea

For Phasmoidea, we used the tree in Robertson et al. (2018). This tree included 7.5% of the extant species (250 of 3284), 32% of the genera (150 of 473), and all three suborders (Robertson et al. 2018). The phylogeny initially included 34 species that were each represented by two terminal taxa (i.e., 284 tips in total). These duplicate taxa were removed before analysis since they could bias rate estimates for state-dependent speciation-extinction models. To address unbiased taxon sampling among clades, we then confirmed that there was a strong positive relationship between the number of phasmid species sampled per subclade and the number of described phasmids per subclade (t = 3.575, $P = 0.002$, r^2 = 0.429, n = 19; Table S3). Subclades (and the lower r^2) are addressed below. Only a single topology (Bayesian consensus tree) was available from the authors.

To determine whether the 250 sampled species had sexually selected weapons we used both the literature and photographs of museum-quality specimens. Male-male combat over

access to females has been recorded in at least two phasmid species: *Diapheromera veliei* of the subfamily Diapheromerinae (Sivinski 1978) and *Eurycantha calcarata* of the subfamily Lonchodinae (Boisseau et al. 2020). Males in these species use their legs, which have enlarged femurs and hooked spines, to fend off their rivals (Sivinski 1978; Boisseau et al. 2020). Similar (sexually dimorphic) leg characteristics have been noted in other Diapheromerinae (Robinson 1968; Sivinski 1978), as well as in taxa associated with the "tree-lobster" ecomorph (Bedford 1975; Boisseau et al. 2020). Thus, we used photographs of male specimens to determine whether enlarged femurs with exaggerated spines (relative to front legs) were present in species in Diapheromerinae and in the tree-lobster genera sampled in the tree. The latter genera included *Acanthoxyla, Canachus, Carlius, Clitarchus, Cnipsus, Dryococelus, Eurycantha, Labidiophasma, Leosthenes, Microcanachus, Thaumatobactron*, and *Trapezaspis* (Buckley et al. 2009; Foottit and Adler 2009). If museum-quality photographs were unavailable for a given species, that species was pruned from the phylogeny. However, if the species was the only representative for a given genus, another species was randomly selected (via a random number generator) from the same genus, and that species was coded instead. Note that when only one species of a genus is sampled in a time-calibrated tree, all species yield the same branch length.

The remaining phasmid species were all coded as not having weapons for two reasons. First, previous reviews of intrasexual weaponry have considered Phasmoidea to be weaponless (Rico-Guevara and Hurme 2019). Second, a literature search using Google Scholar (December 2020) that included the search terms "phasmid" and "combat" did not reveal any additional weapon-bearing phasmid species. However, it did successfully recover the two studies on male combat in phasmids cited above (Sivinski 1978; Boisseau et al. 2020). Coding the remaining phasmids as weaponless could potentially result in some false negatives (i.e., coding a species as not having a weapon when they do). Below, we describe how we incorporate the potential for error with our coding scheme into our analyses.

The overall coding approach used here could also potentially identify some species that do not engage in male-male competition as having sexually selected weapons (i.e., a false positive). For example, male *Eurycantha insularis* have hind legs with enlarged femurs and sexually dimorphic spines (Boisseau et al. 2020). However, radiotelemetry data for *E. insularis* suggests that males engage in scramble competition (Boisseau et al. 2020), making precopulatory male-male competition unlikely. Thus, we used both a more liberal coding scheme in which *E. insularis* was considered to have a sexually selected weapon, and a more conservative coding scheme in which it was considered to be weaponless.

STATISTICAL ANALYSES
SSE Approach
To test the hypothesis that sexually selected weaponry promotes speciation and net diversification, we conducted a series of analyses using two very different approaches. First, we used the SSE framework (state-dependent speciation and extinction: Maddison et al. 2007; FitzJohn et al. 2009; Beaulieu and O'Meara 2016). This approach uses a species-level phylogeny and directly associates character states (e.g., weapon presence vs. absence) with estimated rates of speciation, extinction, and diversification. This approach can explicitly correct for incomplete sampling within a clade, but is still somewhat dependent on the set of species sampled. As an alternative approach, we used the MS estimators (method-of-moments estimators; Magallón and Sanderson 2001). This approach can be used to estimate the overall net diversification rate for each named clade (e.g., genera, families), explicitly incorporating the total number of species in each clade. Phylogenetic regression can then be used to relate diversification rates to the estimated frequency of traits within clades. This approach does not distinguish the separate contributions of speciation and extinction rates to the overall diversification rate for each clade. However, the combination of the MS approach and phylogenetic regression is advantageous in that it can estimate how much variance in diversification rates among clades is explained by the trait of interest. In contrast, SSE methods can only identify a significant association between the trait and rates.

For the SSE approach, we compared five models for each of the three sampled insect clades. We compared two BiSSE models (binary-state SSE; FitzJohn et al. 2009) and three HiSSE models (hidden-state SSE; Beaulieu and O'Meara 2016). The first BiSSE model included two observed states with different rates of transition, speciation, and extinction associated with each observed state. This model tests whether diversification rates differ between lineages with weaponry and those without (i.e., the full BiSSE model). The second BiSSE model treated the two observed states as sharing the same speciation rate and the same extinction rate, but separate transition rates (i.e., the null BiSSE model).

We then compared three HiSSE models. HiSSE models allow one to incorporate hidden states to test the possibility that diversification is driven by an unknown (or unmeasured) factor, instead of (or in addition to) the observed states. For the first HiSSE model, the diversification rate parameters were independent of the presence or absence of weaponry. Specifically, rates differed among the two hidden rate categories, but were identical between the two observed states (i.e., the character independent model with two hidden states; CID-2). Thus, both CID-2 and the full BiSSE models were equally complex, having two states and four free (estimated) diversification-rate parameters. The CID-2

model may be considered a better null hypothesis (Caetano et al. 2018), given that it can help address the potential for high rates of false positives with BiSSE (Rabosky and Goldberg 2015). Next, we conducted a full HiSSE analysis, with two hidden states for each observed state (i.e., 0A, 0B, 1A, 1B). This allowed speciation and extinction rates to vary independently across all four states. Moreover, we allowed transition rates to vary between all observed and hidden states, with the exception of dual transitions. Finally, we conducted another character independent model, but this time we allowed for four hidden states (CID-4 model). The CID-4 model provided an equivalent null hypothesis for the full HiSSE model (Caetano et al. 2018).

All five models were compared using the corrected Akaike information criterion (AICc; Burnham and Anderson 2002) to identify which model had the best fit to the data (i.e., lowest AICc score). Models with AICc that differed by <2 were considered to have equivalent support (Burnham and Anderson 2002). All SSE analyses were conducted in the package HiSSE (version 1.9.6; Beaulieu and O'Meara 2016), using R version 3.6.0 (R Core Team 2019).

SSE models can explicitly incorporate incomplete taxon sampling. Thus, for all SSE analyses we corrected for the proportion of unsampled taxa. The proportion of sampled taxa was estimated by dividing the total number of species in the tree by the total number of species in the clade, as estimated by the Catalogue of Life (Roskov et al. 2014). We also assumed that the presence of weaponry did not bias how taxa were sampled. Thus, if 10% of the sampled species in the tree had weapons, we assumed that 10% of the species in the entire clade had weapons. We think that this is a reasonable assumption because the phylogenies used in this study were built to investigate hypotheses unrelated to the evolution of weaponry.

To correct for incomplete taxon sampling, SSE models assume that samples included in the tree are random (FitzJohn et al. 2009). For Scarabaeoidea and Phasmoidea, we confirmed that there was a strong, positive relationship between the number of species sampled per subclade and the number of described species per subclade (Scarabaeoidea: $t = 14.379$, $P < 0.001$, $r^2 = 0.958$, Phasmoidea: t = 3.575, $P = 0.002$, $r^2 = 0.429$). Overall, this relationship indicated that the sampling was taxonomically unbiased (i.e., if species are sampled randomly, then the most species should be sampled from the largest subclades and the fewest from the smallest subclades). As noted above, the sampling of species among higher taxa within subclades is not necessarily perfectly proportional (e.g., within a family some subfamilies may be overrepresented relative to others), but this should not prevent us from finding a significant association between weapons and diversification using SSE analyses.

We note that one phasmid group (Lanceocerata) was overrepresented relative to its richness, which was reflected in the

relatively low r^2 value. Nevertheless, separate SSE analyses of Lanceocerata produced qualitatively similar results as other phasmid subclades (e.g., Lonchodinae; see Results; Table S5).

For the Coreidae + Alydidae clade, we were unable to conduct a similar analysis of subclades because there was a poor match between taxonomy and phylogeny in the clade (Forthman et al. 2019, Forthman et al. 2020). Thus, because many of the sampled tribes were not monophyletic, it was uncertain what genera could be assigned to them, and so their actual species richness was unclear. However, the sampled species represented broad sampling from Australia, Asia, Africa, and North America (Emberts et al. 2020), so the sampling should be taxonomically unbiased.

The SSE framework is known to have some limitations. For example, simulations have shown that SSE methods can give spurious results when a trait has a frequency of 10% or less (Davis et al. 2013; but see Gamisch 2016). Unfortunately, only 4% of all phasmids were estimated to have sexually selected weapons. Importantly, this low frequency among species by itself suggests that these weapons may not increase diversification in this group. We therefore conducted separate SSE analyses on two phasmid subclades: Lanceocerata (49 sampled species, ∼8% with weaponry; Fig. 2) and Lonchodinae (30 sampled species, ∼13% with weaponry; Fig. 2). SSE methods may also have limited power when analyzing clades with <200 sampled species (Davis et al. 2013; but see Gamisch 2016). To address this concern, we verified that we could detect differences in diversification in the smaller clade (Lonchodinae; 30 species, four of which have weapons). Specifically, we distributed weapons among the tips in a way that seemed most favorable to the hypothesis that weapons drive diversification, and we found that we were able to obtain significant results (details in Table S2).

MS Estimators

For our second approach, we used the method-of-moments estimator (MS estimator hereafter; Magallón and Sanderson 2001). We first estimated diversification rates of named subclades (e.g., families). We then used phylogenetic generalized least squares (PGLS) regression (Martins and Hansen 1997) to test the relationship between diversification rates and the estimated proportion of species with weaponry in those subclades. If weaponry promotes diversification, then there should be a significant, positive relationship between the proportion of species with weapons in a subclade and the rate at which the subclade diversified. We implemented PGLS analyses in the R package *caper* (version 1.0.1; Orme et al. 2013). Values of λ were estimated using maximum likelihood, unless noted otherwise. To conduct these analyses, we first identified named subclades within each of the three sampled clades (see below). We then determined the stem age of each subclade and its species richness. With this
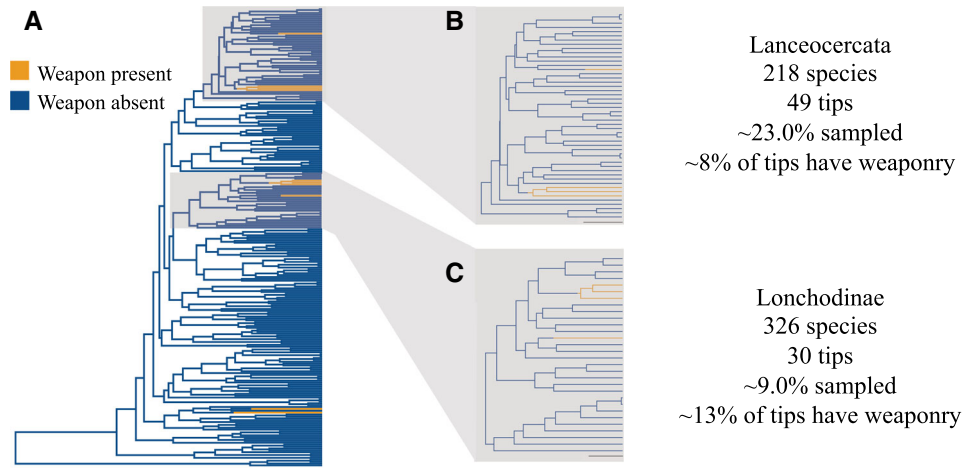
Figure 2. Phylogeny of Phasmatodea used, including all species (A) and two subclades, Lanceocercata (B) and Lonchodinae (C). Below the name of each subclade, we give the total number of described species in the subclade (estimated using Robertson et al. 2018), the number of species sampled in the tree (tips), the percentage of species sampled, and the percentage of sampled species that were scored as having weapons. Sexually selected weaponry has evolved twice within both subclades according to the depicted stochastic character simulations (which assume equal rates). These simulations were conducted with *phytools* using the make.simmap function. The phylogenies are time calibrated, and each respective scale bar at the bottom of the phylogenies indicate the branch lengths associated with 10 million years.

information, we calculated the diversification rate of each subclade using the stem-group estimator equation (equation 6 in Magallón and Sanderson 2001). We used the stem-group estimator because it is unaffected by incomplete species sampling within clades (Meyer and Wiens 2018), and also appears to be robust to incomplete sampling among clades (Scholl and Wiens 2016). We used three extinction fractions ($\epsilon = 0$, 0.5, and 0.9). The extinction fraction is the assumed ratio of extinction to speciation rates. This is a correction for clades that are entirely unsampled because they are extinct (Magallón and Sanderson 2001). This correction does not require that all clades have the same extinction rate (e.g., in simulations, the MS estimator can perform well even when the same extinction fraction is assumed for all clades but different clades have different extinction rates; Meyer and Wiens 2018).

This approach can incorporate all described species in each clade and only requires estimates of subclade ages and species richness. Moreover, it does not require constant rates within or among clades to accurately estimate diversification rates (Meyer and Wiens 2018; Meyer et al. 2018). Specifically, simulations show that this approach can give accurate estimates of diversification rates for clades when rates differ strongly between subclades (Meyer and Wiens 2018), when rates change strongly over time within clades (Meyer et al. 2018), and when rates are much faster in younger clades (Kozak and Wiens 2016). Moreover, this approach does not assume a limited number of rates across the tree, like SSE methods and BAMM (Bayesian Analysis of Macroevolutionary Mixtures; Rabosky 2014). For example, SSE methods generally assume only 1 or 2 distinct rates for each observed state, whereas BAMM tends to estimate only

two or three distinct rates across large simulated trees with >10 distinct rates and hundreds to thousands of species (Meyer and Wiens 2018). The MS estimators estimate a number of distinct rates across the tree equal to the number of clades used (and do not require constant rates within these clades). However, the ability of this approach to use named clades when taxon sampling is incomplete requires a general match between taxonomy and phylogeny (e.g., the species richness of a genus will be incorrect if the genus is not monophyletic). Therefore, because of the high inconsistency between taxonomy and phylogeny in the Coreidae + Alydidae clade (Forthman et al. 2019, Forthman et al. 2020), we were unable to apply the MS estimators to this group.

For Phasmatodea, we used the same 23 subclades identified in Robertson et al. (2018). Robertson et al. (2018) provided stem ages and species richness for 19 of these named subclades (including ~84% of the currently recognized species; Roskov et al. 2014). Because of incongruence between the taxonomy and phylogeny, we could not estimate species richness for the remaining four subclades. Thus, we removed these four subclades from our MS analyses, leaving 19 subclades (details in Table S3). Sexually selected weapons are not known to be present in the four excluded subclades.

For Scarabaeoidea, we used the 26 families identified in the Catalogue of Life (Roskov et al. 2014). The phylogeny reported in Ahrens et al. (2014) included 20 of these families. These 20 families represent >99% of the currently recognized species of Scarabaeoidea (Roskov et al. 2014). Among these 20 families, 12 were not monophyletic. In these cases, we combined polyphyletic and/or paraphyletic families with others to form larger

subclades. This ultimately resulted in 11 unique subclades (details in Table S4). The number of species within each subclade was estimated via the Catalogue of Life (Roskov et al. 2014) and the stem age of each subclade was estimated from the time-calibrated tree (Ahrens et al. 2014; BEAST run 6).

We next estimated the proportion of species within each subclade that had sexually selected weaponry. We specifically used the sampled species in the phylogenies to estimate the proportion of species in each subclade that have weapons (Tables S3, S4). For example, four out of the five sampled species in the subclade Bolboracertidae + Passalidae had sexually selected weapons. Thus, we assumed that 80% of the species in this subclade had weapons (Table S4).

There are many possible sources of error in estimating these frequencies. First, the proportion of weapon-bearing species represented in the phylogeny may not accurately reflect the true proportion. For example, some species of beetles in Geotrupidae (Ohde et al. 2018) are known to have weapons. However, the methodology employed here estimates the Geotrupidae clade to be weaponless (Table S4). Second, some species coded as having weapons may not actually have weapons, or vice versa. For example, species with weapon-like structures may not use them as weapons. Alternatively, coding errors could have occurred because of weapon polymorphism (Buzatto et al. 2014). Thus, photographed specimens that were used to assign weaponry may have been minor morphs that lacked the weapon completely. To help address this issue, we inspected all the digital specimens of males that were available from our noted sources. Nevertheless, it is possible that only minor male morphs were present in these repositories. Third, despite our overall proportional sampling of species among subclades, if sampling within subclades does not reflect the relative species richness of higher taxa within that subclade (e.g., subfamilies within a family), estimated trait frequencies could also be somewhat distorted. These many potential sources of error may sound troubling. However, simulations suggest that relationships between trait frequencies and diversification can be robust to at least 20% error in estimating frequencies for each clade (Moen and Wiens 2017).

We also tested the robustness of our main results to a similar level of error in estimated frequencies. We conducted 100 replicates each for Scarabaeoidea and Phasmatodea. For each replicate, the exact proportions used for each subclade were generated by randomly selecting a proportion from a truncated uniform distribution. The specific distribution used for each subclade was determined by applying a 20% error rate in either direction. Thus, if 50% of the species in a clade were estimated to have weapons, we allowed the distribution to range from 30% to 70%. However, we did not allow ranges to be negative or exceed 100%. Thus, if 0% of a clade was estimated to have weapons,

we allowed for the uniform distribution to range from 0% to 20%.

We then conducted PGLS analyses on each replicate. For each replicate, the independent variable was the estimated proportion of species in each subclade with weapons, whereas the dependent variable was the subclade's estimated diversification rate (with $\epsilon = 0.5$). We conducted PGLS assuming a λ value of 0.001 and (in an alternative set of analyses) a value of 1.00 (i.e., a low or high value). Values were assigned because the PGLS maximum likelihood function was unable to estimate λ in some cases. We confirmed that our results were similar regardless of which λ value we used (see Results, Fig. S1). We emphasize the low values because the observed λ values for the observed data were generally low. Overall, we considered our results to be robust to this level of error if $\geq 95\%$ of simulation replicates reached the same conclusion about the relationship between diversification and weaponry as our observed results (i.e., a significant positive relationship, a significant negative relationship, or no relationship).

In the main text, we report the analyses using the most liberal coding scheme (i.e., the coding scheme yielding the highest percentage of weapons among species in the subclade). The results of our more conservative weapon-coding schemes are qualitatively similar and are reported in the supporting information (Tables S5 and S6). The data, phylogenies, and R code needed to replicate our analyses is available on Dryad (Emberts and Wiens 2021b).

Results

To assess if weapons influenced diversification rates in each insect clade, we first compared five state-dependent speciation and extinction (SSE) models (BiSSE, BiSSE null, CID-2, HiSSE, and CID-4). Neither BiSSE nor HiSSE was ever the best-fitting model (Table 1). Instead, depending on the analysis, the best-fitting model was either the null BiSSE model or one of the character-independent models (i.e., CID-2 or CID-4). For leaf-footed and broad-headed bugs (Coreidae + Alydidae; Table 1), the best fitting model was the null BiSSE model, which suggests that lineages with and without weapons have similar overall rates of speciation and net diversification. For scarab beetles (Scarabaeoidea) and the order including the stick insects (Phasmatodea), the best fitting model was a character-independent model (Table 1). These character-independent models suggests that variation in diversification rates across the tree is unrelated to weaponry. Results were similar using alternative trees for beetles (Table S1) and alternative coding schemes for all three clades, with only null BiSSE or character-independent models supported (Table S5). Thus, for all three insect clades, the presence of sexually selected

Table 1. Results of state-dependent speciation and extinction (SSE) models.

	Coreidae + Alydidae ($n = 53$)		Scarabaeoidea ($n = 144$)		Phasmatodea (all, ($n = 243$)		Phasmatodea (Lanceocercata clade, $n = 49$)		Phasmatodea (Lonchodinae clade, $n = 30$)	
	AICc	ΔAICc	AICc	ΔAICc	AICc	ΔAICc	AICc	ΔAICc	AICc	ΔAICc
BiSSE	395.2	5.4	1547.2	30.7	2048.0	60.8	382.5	2.8	259.6	16.3
Null BiSSE	**389.8**	**0.0**	1542.4	25.9	1991.7	4.5	380.1	0.4	**243.3**	**0.0**
CID-2	393.6	3.8	1543.2	26.7	**1987.2**	**0.0**	**379.7**	**0.0**	246.3	3.0
HiSSE	423.3	33.5	1553.5	37.0	2014.9	27.7	404.7	25.0	308.8	65.5
CID-4	480.0	90.2	**1516.5**	**0.0**	2001.1	13.9	384.6	4.9	260.4	17.1

These models tested whether lineages with sexually selected weapons had different rates of speciation, extinction, and diversification relative to those without. The corrected Akaike information criterion (AICc) was used to determine the best fitting model. For all analyses, the best-fitting model was either the null BiSSE model or one of the character independent models (CID-2, CID-4), but was never the BiSSE or HiSSE models, which would suggest trait-dependent diversification. Thus, there was no evidence that weapons impact diversification in these groups. ΔAICc (rounded to the nearest tenth) compares a model's AICc score to the best model (boldfaced).

weaponry did not appear to increase rates of speciation nor net diversification.

Given the low frequency of weapons in phasmids, we also conducted separate SSE analyses on two phasmid subclades (Lanceocercata and Lonchodinae). Sexually selected weaponry did not appear to promote speciation nor net diversification in these two subclades either (Table 1). For Lanceocercata, the best fitting model was the CID-2 model. However, the null BiSSE model was similar (i.e., a competing model; ΔAICc < 2). Both models suggest the absence of weapon-dependent diversification. For Lonchodinae, the best-fitting model was the null BiSSE model. Thus, these two subclades showed that lineages with and without weapons have similar rates of speciation and net diversification. Importantly, all the SSE analyses (regardless of our weapon coding scheme) revealed that models in which sexually selected weaponry promoted speciation and net diversification never had the best fit (Table 1; Table S5).

We also conducted PGLS regression to test the relationship between diversification rates of subclades (estimated from the MS estimators) and the proportion of species within that subclade with sexually selected weapons. We conducted these analyses for scarab beetles (Scarabaeoidea) and phasmids (Phasmatodea). We found no significant relationships between diversification rates and the presence of weaponry (Table 2; Fig. 3), concordant with the SSE analyses. Results were also non-significant when using an alternative weapon-coding scheme (Table S6).

There is undoubtedly some error associated with estimating the proportion of species in each subclade that have weapons. Therefore, we simulated up to 20% error in the estimated proportions for each subclade and ran 100 additional PGLS analyses for each clade. For both clades examined (Scarabaeoidea and Phasmatodea), almost all analyses (≥96%) indicated no significant relationship between the diversification rate and the frequency

Table 2. Results of phylogenetic regressions testing relationships between diversification rates and frequency of sexually selected weapons among species.

	ϵ	slope	t	P	r^2
Scarabaeoidea	0.0	0.011	1.747	0.115	0.253
	0.5	0.011	1.728	0.118	0.249
	0.9	0.011	1.707	0.122	0.245
Phasmatodea	0.0	0.100	1.440	0.168	0.108
	0.5	0.108	1.559	0.137	0.125
	0.9	0.101	1.809	0.088	0.161

Diversification rates (dependent variable) were estimated using the MS estimators. The proportion of species with sexually selected weapons in each subclade was the independent variable. There were 11 subclades of scarab beetles analyzed and 19 subclades of stick insects. These results are based on liberal coding (maximizing the number of species considered to have these weapons). Results using conservative coding were similar, and are given in Table S6.

of weaponry, while ≤4% of the simulations indicated a significant, positive association between diversification and weaponry (Fig. 3). The results were similar regardless of whether we assigned a λ value of 0.001 (Fig. 3) or 1.000 (Fig. S1). Thus, our main PGLS results (Table 2; Fig. 3) were robust to considerable error in estimating the proportion of species with weapons in each subclade. These simulations also showed that these data would have sufficient power to detect a significant relationship, if the estimated trait frequencies were more consistent with the hypothesis that weapons increase diversification rates.

Discussion

Sexual selection has long been though to drive diversification, but most of this literature has emphasized female choice. Here, we
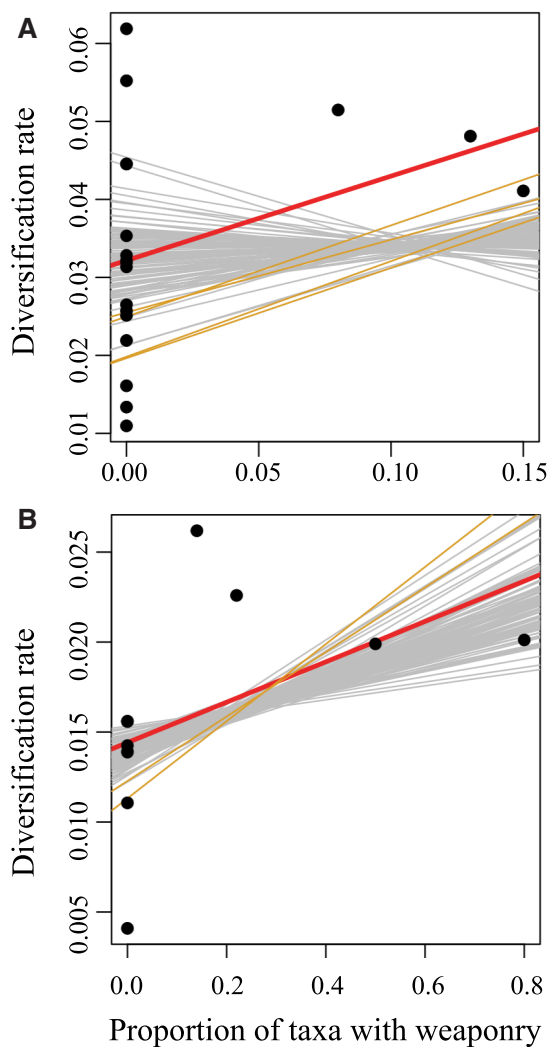
Figure 3. Relationships between diversification rates and the presence of sexually selected weapons among subclades of stick insects and relatives (A) and scarab beetles (B). Diversification rates (species per million years) were estimated using the method-of-moments (MS) estimators with a relative extinction fraction (ϵ) of 0.5. The red regression lines correspond to results using the estimated proportion of species with weapons (our main PGLS analyses). Both red regression lines indicate positive relationships, but neither is strong enough to be statistically significant (Table 2). In both groups, the subclades with the highest diversification rates lack weaponry or have weapons at low frequencies among species. The grey and gold regression lines show results of 100 simulation replicates (when assuming a λ value of 0.001) that incorporated simulated error into the estimates of the proportion of species with weaponry. Gray lines correspond to non-significant relationships ($\geq$96%), whereas gold lines correspond to significant relationships ($\leq$4%). Results of simulated replicate regressions that assume a lambda value of 1 are visualized in Figure S1 and are qualitatively similar to those visualized here.

investigated whether traits associated with male-male competition (i.e., an alternative mechanism of sexual selection) have promoted speciation and net diversification in three insect clades. We found no evidence that weapon-bearing lineages in these clades have higher rates of net diversification when compared to their weaponless relatives. These results suggest that sexually selected weapons are not a major driver of speciation or diversification in these clades.

We recognize that these results might be dismissed as being negative and only for three clades. However, we demonstrated repeatedly that our analyses had sufficient power to detect a significant effect, including the SSE analyses of the smallest clade (30 sampled species; Table S2) and all our PGLS analyses (Fig. 3). Thus, our negative results were caused by the distribution of the traits, and not a weakness of the tests. Furthermore, each of the clades that we examined included over 2,800 species. One clade (Scarabaeoidea; 39,717 species) included more species than all amphibians, birds, mammals, and non-avian reptiles combined. Of course, other clades may show different patterns, but we do not know of other, larger clades in which sexually selected weapons are widespread among species.

Moreover, the fact that all of our results were consistent with one another allows us to be fairly confident in our results, despite limitations associated with each method. For example, a major critique of SSE methods is that they have a high rate of false positives (e.g., Rabosky and Goldberg 2015). However, since we do not have a positive result, this critique clearly does not apply here. Another limitation is that some of our tips could have been coded erroneously. We took multiple steps to address this potential source of error. For the SSE analyses, we used both a liberal and a conservative approach when coding sexually selected weaponry. For the MS analyses, we explicitly incorporated potential error into the estimation of weapon frequencies within clades. Our results were similar regardless of the coding scheme and almost all weapon frequency estimates (Tables S5 and S6), suggesting that sexually selected weapons are not a major driver of speciation or diversification in these clades. Nevertheless, we emphasize that we cannot completely rule out the possibility of effects that are weak or very localized.

There are several plausible scenarios that could explain why we did not find the expected pattern of increased diversification associated with sexually selected weapons (e.g., Tinghitella et al. 2018; Parrett et al. 2019). Large-scale diversification analyses (such as those conducted here) can detect major drivers of speciation and net diversification across a clade. However, if the effects of weaponry are weak or localized, then the effect may be drowned out by other variables that impact speciation and diversification rates. For example, a certain physiological or genetic

mechanism might be required for male-male competition to facilitate reproductive isolation (Tinghitella et al. 2018), and this mechanism could be relatively uncommon (e.g., found within a single genus). In this case, male-male competition would not be a major driver of diversification for the entire clade. Yet, we also found that highly localized effects among very few species can be detected using HiSSE (4 of 30; Table S2). Furthermore, even though we suggested above that the effects of weapons could be drowned out by other variables, the methods we used can detect when multiple traits significantly impact diversification rates. For example, HiSSE is specifically designed to detect impacts of multiple traits (Beaulieu and O'Meara 2016) and the combination of MS estimators and PGLS can detect significant effects of many traits simultaneously (e.g., 5 traits among animal phyla: Jezkova and Wiens 2017; up to 7 traits across land plants; Hernández-Hernández and Wiens 2020). It is also possible that male-male competition promoted speciation but only during certain periods in the past. Such fluctuating effects might be particularly difficult to detect. Finally, another reason why we might have been unable to detect the effects of weaponry on speciation at this scale could be related to ecology. For example, precopulatory sexual selection may promote speciation, but recently diverged species may be unable to coexist because they are ecologically similar (see Cooney et al. 2017). Thus, sexually selected weapons may promote speciation, but the overall production of species may be capped by ecological constraints. In this scenario, clade-wide analyses (such as those conducted here) might be unable to detect the role of sexually selected weaponry on speciation. At the same time, it seems that a positive effect of sexually selected traits on diversification should at least be present among a few closely related species, which our study could potentially have found (Table S2) but did not. Nevertheless, future studies that test whether weapons influence reproductive isolation and speciation among populations and closely related species would still be valuable, especially given that the effects of sexual selection on diversification might fade at deeper timescales (Kraaijeveld et al. 2011).

It is also possible that male-male competition is an important driver of diversification in these insect clades, but the specific type of trait that we examined here (i.e., weaponry) is not. For example, species may engage in postcopulatory male-male competition (Birkhead and Pizzari 2002). Thus, we restrict our conclusions to precopulatory weapons. We acknowledge that postcopulatory male-male competition might influence diversification rates, even when weapons do not. For example, a previous study showed that polyandrous insect lineages are more species-rich than monandrous insect lineages (Arnqvist et al. 2000). This association suggests that postcopulatory sexual selection may drive net diversification in insects. However, the degree to which male-male competition and/or female choice are responsible for driving this pattern is unclear. Interestingly, there is no overlap in the clades examined in the study by Arnqvist et al. (2000) and those examined here, and most of the clades examined in Arnqvist et al. (2000) were relatively small (90% with <1000 species).

In summary, we found no evidence that lineages with sexually selected weapons have higher rates of speciation or net diversification than those without. These results strongly suggest that sexually selected weapons are not a major driver of speciation and net diversification in the insect clades studied. However, these results cannot rule out the possibility of a weak effect, or an effect only among very closely related species in these clades. Although our study includes only three clades, we know of no other group in which weapons have been shown to influence diversification (in insects or other groups). Thus, our study raises the question of whether increases in diversification associated with precopulatory sexually selected traits (when present) are limited to sexually selected ornaments.

AUTHOR CONTRIBUTIONS
Z.E. conceived the study, collected the data, performed the statistical analyses, and wrote the first draft. J.J.W. contributed to study design, statistical analyses, and writing.

CONFLICTS OF INTEREST
The authors declare no conflicts of interest.

DATA ARCHIVING
All the data, phylogenies, and code used for our analyses are available on Dryad (https://doi.org/10.5061/dryad.fqz612js3).

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Supporting Information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Table S1. Results of state-dependent speciation and extinction (SSE) models for all available Scarabaeoidea trees from Ahrens et al. (2014).

Table S2. Testing for power in a subclade of phasmid insects.

Table S3. Summary of Phasmatodea subclades.

Table S4. Summary of Scarabaeoidea subclades.

Table S5. Results of state-dependent speciation and extinction (SSE) models when using a more conservative weapon coding scheme.

Table S6. Results of phylogenetic regressions testing relationships between diversification rates and sexually selected weapons among species, using a more conservative weapon coding scheme.

Figure S1. Relationships between diversification rates and the presence of sexually selected weapons among subclades of stick insects and relatives (A) and scarab beetles (B) showing effects of assuming a different λ value in the simulated error replicates.